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THE UNIVERSITY OF MICHIGAN

VOL. XVII, No. 3, pp. 77–121 (2 pls., 6 figs.) OCTOBER 20, 1961

A NEW SPECIES OF *BILLINGSITES*, AN ASCOCERATID CEPHALOPOD, FROM THE UPPER ORDOVICIAN OGONTZ FORMATION OF MICHIGAN

BY

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CONTENTS

INTRODUCTION

ENIGMATICALLY, the cephalopods on which this paper is based have been known in publication for thirty-five years but they are new. Because the previous references were *nomina nuda,* the species has remained technically undescribed and scientifically unknown. These fossils belong to a curious group of nautiloids, the Ascoceratida, which overcame the handicap of an unwieldy conch by truncation, casting off the earlier, impeding stages of the shell to adapt to a new mode of life. Although it has long been suspected that the Ordovician representatives, like their Silurian descendants, formed a cyrtoconic phragmocone in their youthful stages, each specimen previously described has consisted of only the expanded adoral part of the conch, the segment retained by the animal after the final truncation. One

of the specimens described here is the first Ordovician ascoceratidan discovered which kept a part of the cyrtoconic phragmocone.

Because the terminology of these cephalopods is not only rather extensive but also varies from author to author, there is a section to explain the terms that I use. In the systematic descriptions, the nature of the cephalopods and their classification is discussed under the order, family, and genus for the purpose of showing the position of the new species. Treatment of the genus *Billingsites* includes a key to the well-substantiated species now assigned to it.

Longitudinal sections of selected specimens of the new species reveal significant details of the internal organization. A few specimens show ventral markings which appear to represent aponeurotic bands in the adult living chamber. From information available, it is possible to reconstruct the cephalopod with some degree of assurance. The paper closes with certain inferences and hypotheses regarding the animal's mode of life, particularly with reference to the changes of buoyancy engendered by truncation.

As might have been expected, the first published mention of the occurrence of *Billingsites* in Michigan was by August F. Foerste, the leading authority of his day on cephalopods, who did outstanding work on the Ascoceratidae in America. As Dr. George M. Ehlers informs me, Dr. Foerste willingly gave of his time to anyone with a problem involving cephalopods and helped with the identification of many specimens in the Museum of Paleontology of the University of Michigan. Still, today, in looking through the drawers of Paleozoic fossils, one occasionally comes across specimens accompanied by the notation "Send to Foerste"—nostalgic reminders of the generosity of a great paleontologist and the high regard in which he was held by his contemporaries. Yet it was also characteristic of Dr. Foerste that he could be persuaded to accept responsibility for more species than he could possibly describe, even at his tremendous tempo of investigation and volume of publication.

For one of the fossils described here, UMMP No. 9831, the Museum of Paleontology has a catalogue card stating that this specimen was to be the holotype of a species to be described by Dr. Foerste under the name *"Billingsites newberryi noquettensis."* Further, R. C. Hussey in 1926 and 1950 used this name in faunal lists and illustrated the specimen in 1926. From 1924, when he first acknowledged the existence of the species, until his death in 1936, Dr. Foerste evidently did not get around to describing the Michigan *Billingsites*. It seems fitting, as a tribute to his yeoman work on *Billingsites* and his recognition of the Michigan cephalopod as new, to use Dr. Foerste's suggested name *"noquettensis"* and to utilize his intended holotype as the actual holotype of the new species.

I gratefully acknowledge the kind suggestions by Dr. George M. Ehlers and the critical review of the manuscript by Dr. Lewis B. Kellum and Dr. Chester A. Arnold.

Specimens are catalogued and deposited in the Museum of Paleontology of the University of Michigan.

LOCALITY

All specimens are from the same locality and were collected by R. C. Hussey prior to the publication of his paper in the *Contributions from the Museum of Geology,* Vol. 2, in 1926. Only one specimen, UMMP No. 9831, which was illustrated by Hussey in 1926 (Pl. 8, Figs. 10–12), was catalogued before 1961. The other specimens had been retained in the general collection, accompanied by data on the occurrence and collector.

Field in NW¼ sec. 25, T. 39 N., R. 21 W., east of the Swedish Church and about ½ mile south of the home of J. B. Stratton (located in SW¼ sec. 24 of same twp.), west side of Stonington Peninsula, Delta Co., Michigan. Locality 8 of Hussey (1926, pp. 116–17, 139). Upper Ordovician Richmond group, Ogontz formation (Ogontz member of the Stonington beds in Hussey's classification).

PREVIOUS REFERENCES TO MICHIGAN SPECIMENS

As pointed out in the introduction, A. F. Foerste was the first to refer to these cephalopods. He wrote (1924, p. 222): "Specimens [of *Billingsites*] occur also in the Richmond of Bay de Noc peninsula, east of Escanaba, Michigan."

Two years later, R. C. Hussey (1926, p. 182), placed the name "*Billingsites newberryi noquettensis*" in faunal lists of the Ogontz formation, and illustrated (Pl. 8, Figs. 10–12) one specimen, UMMP No. 9831.

Subsequently, Foerste made three references to the occurrence: 1928*b* (p. 223), "*Billingsites* is known . . . in the Ogontz division of the Stonington member east of Escanaba in northern Michigan . . ."; 1929*a* (p. 40), "*Billingsites* occurs in the Richmond of Anticosti, Michigan, Indiana, Ohio, and in the Maquoketa phase of the Richmond in eastern Iowa"; and 1929*b* (p. 157), "*Billingsites* is widely distributed on the American continent, occurring . . . on the peninsula east of Escanaba in northern Michigan, . . ."

Miller (1932*b*, p. 27), in his revision of the group, stated: "Also, Foerste has mentioned in his recent publications that unnamed representatives of '*Billingsites*' occur in . . . the Ogonotz [sic] division of the Stonington (Richmond) of the peninsula east of Escanaba in northern Michigan. . . . Part of these forms doubtlessly represent *Billingsites* s.s. and part the genus described below as *Schuchertoceras,* but the published information in regard to them is not sufficient to allot them."

In 1950 (p. 20) Hussey again listed *"Billingsites newberryi noquettensis* Foerste" from the Ogontz formation. In 1952 (p. 51) he without doubt had this species in mind when he included *"Billingsites newberryi* (Billings)" in his faunal list of the Ogontz formation.

The specimens unquestionably belong to the genus *Billingsites* as restricted by Miller in 1932. The species *newberryi,* however, was quite properly assigned to his new genus *Schuchertoceras* by Miller (1932*b*, p. 31). Hence, *"noquettensis"* must be used as a specific rather than a subspecific name, and the designation of *"Billingsites newberryi"* by Hussey in 1952 is entirely erroneous.

TERMINOLOGY OF ASCOCERATID CEPHALOPODS

Only the terms which have special meaning as used for ascoceratid cephalopods need be discussed. An extensive glossary of cephalopod terms is offered by Flower (1946, pp. 57–68). Figure 1 is labeled with certain of the terms applied to ascoceratids:

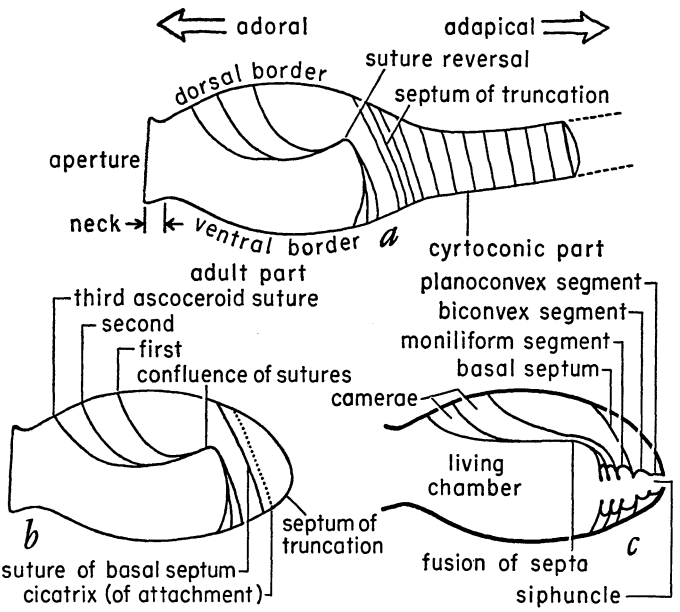

FIG. 1. Hypothetical conch of an ascoceratid cephalopod to illustrate certain terms used in this paper. *a,* left side of specimen consisting of adult part and incomplete cyrtoconic part of conch. *b,* adult part of conch after truncation. *c,* vertical section through adult part of conch; siphuncular segments are somewhat exaggerated.

adapical—toward the apex or initial end of the conch; in truncated forms, used to denote toward the earlier-formed part of the conch.

adoral—toward the aperture, opposite to adapical.

adult part—ovoid part of conch in *Billingsites,* which separates from the earlier-formed cyrtoconic phragmocone.

apex—the earliest-formed part of the conch as retained; in a complete conch, the initial shell deposit, but in a truncated conch, the septum of truncation.

ascoceroid septum—septum which forms an ascoceroid suture with the outer wall.

ascoceroid suture—sigmoid suture which has its dorsal part extended adorally to form a broad saddle; from the ventral border, such a suture on each side rises dorsally and is ventrally recurved at the suture reversal before continuing adorally and rising to the dorsal border.

basal septum—septum present in some genera between the septum of truncation and the first ascoceroid septum; may be somewhat sigmoid, but never with a suture reversal.

camera—a compartment between septa, in life presumed to have been filled with gas; in adult parts of conchs, camerae may not extend from dorsal to ventral border because of fusion of adjacent ascoceroid septa. Also called "float chambers."

cicatrix or *cicatrix of attachment*—mark left after truncation, a narrow annulus along which adult and cyrtoconic parts of the conch formerly were united; the cicatrix establishes the distal limit of the septum of truncation.

confluence of sutures—joining of ascoceroid sutures on the sides of the adult part of the conch.

connecting ring—calcareous (originally probably containing much conchiolin, as in *Nautilus*) tube secreted by the siphon, together with the septal necks forming the siphuncle. See siphuncular segments.

cyrtochoanitic—siphuncle with expanded segments. See siphuncular segments.

cyrtocone or *cyrtoconic part*—long, gently curved juvenile part of the conch, lost from the adult part by truncation.

fusion of septa—joining of ascoceroid septa, forming confluence of sutures at the distal edges of the septa.

living chamber—part of the conch opening through the aperture and bounded adapically by the last-formed septum; contrasted with the phragmocone.

mixochoanitic—combination of earlier-formed suborthochoanitic and later-formed cyrtochoanitic siphuncular segments in the same conch.

neck—collar-like adoral contracted section of the adult part of the conch, between the aperture and the ovoid part of the adult conch.

phragmocone—septate or chambered part of the conch, as contrasted with the living chamber; used to refer to the gas space inside the conch in discussion of buoyancy.

septal neck—adapically-directed part of septum which, together with the connecting rings, forms part of siphuncle.

septum of truncation—rear wall of the adult part of the conch, the septum retained adapically with truncation and outlined by the cicatrix.

siphuncular segment—a recognizable unit of the siphuncle, usually extending from one septum to the next; junctions of segments not at septa are thought to denote the former positions of septa lost during phylogeny.

biconvex—expanded in all planes, but with septal necks not greatly reflected.

moniliform—greatly expanded in all planes, the septal necks greatly reflected or recumbent and adnate with connecting rings.

planoconvex—dorsally straight, but expanded in all other directions.

prebasal—lying between the septum of truncation and the basal septum.

suborthochoanitic—siphuncle with segments only slightly expanded or planoconvex.

suture reversal—point on the side of the adult part at which the ascoceroid suture, extending upward from the ventral border, is sharply recurved and again directed downward before continuing adorally to form the dorsal saddle. (*Lateral angle* of Flower, 1946, p. 65).

truncation—natural process by which an ascoceratid cephalopod sheds the cyrtoconic part of the conch; also applied to shedding of earlier-formed parts of the cyrtocone during ontogeny.

SYSTEMATIC DESCRIPTION

Order ASCOCERATIDA

The classification used here for suprageneric categories is that outlined by Flower and Kummel (1950). Their order, Ascoceratida (p. 610) corresponded to Hyatt's Mixochoanites as used in previous comprehensive works on these cephalopods (Miller, 1932*b*; Flower, 1941).

This group of cephalopods has been called "très-bizarres" (Barrande, 1867, p. 334), "enigmatic" (Dunbar, 1924, p. 198), "little group of aberrant forms" (Miller, 1932*b*, p. 9), "anomalous cephalopods" (Flower, 1941, p. 523), and "eigenartigste Gestalten" (Tobein, 1949, p. 307). It is characterized by formation of an expanded adult section followed by truncation of the earlier cyrtoconic part of the phragmocone. Although only the Middle Silurian forms were known then, Barrande in 1877 recognized the sig-

nificance of truncation and wrote (p. 303): "Nous devons considérer la troncature naturelle de la pointe de la coquille comme inhérente à ce type, et comme constituant un de ses caractères distinctifs." Later, Miller (1932*b*, p. 56) and Flower (1941, p. 528) discussed truncation in Ordovician genera also. Flower and Kummel (1950, p. 610) made it part of the ordinal diagnosis.

Another feature common to all Ascoceratida is the development of expanded siphuncular segments late in ontogeny. Indeed, it was the exceptional association of suborthochoanitic and cyrtochoanitic segments that suggested the old designation of Mixochoanites.

The order contains three families. The ancestral Hebetoceratidae (Fig. 2) has a known range from Chazy (lower M. Ord.) to Richmond (Upper U. Ord.). It gave rise in Middle Ordovician time to the Choanoceratidae and in Upper Ordovician to the Ascoceratidae, both of which extended to Middle Silurian.

Although the Hebetoceratidae developed curved septa and sutures that extended forward on the dorsal border of the adult conch, it did not attain ascoceroid sutures. On the basis of its septa it can be differentiated from the other families. *Montyoceras* and *Hebetoceras* were relatively slender, with the adult section not inflated (Fig. 2). *Probillingsites* and *Shamattawaceras* were ovoid as adults, with sutures extending farther adoral dorsally than in earlier genera.

The Choanoceratidae (not shown in Fig. 2) have slender cyrtoconic conchs, deeply conical septa, and fusion of septa below the siphuncle instead of above it, as in the Ascoceratidae.

The Ascoceratidae are characterized by ascoceroid sutures.

Family Ascoceratidae

Within the family Ascoceratidae (Fig. 2) evolutionary changes have been established in detail in the very significant works of Miller (1932*b*, pp. 56–59) and Flower (1941, pp. 527–39). *Schuchertoceras,* the oldest genus, appears to have developed in Upper Ordovician time from *Probillingsites,* from which it differs in having ascoceroid septa. From it evolved, in sequence, *Lindstroemoceras, Parascoceras, Pseudascoceras,* and *Ascoceras. Billingsites* seems to have descended from *Schuchertoceras,* and *Aphragmites* and *Glossoceras* from *Ascoceras.*

Evolution is demonstrated in several features. The strongly ovoid adult conch (in *Schuchertoceras, Billingsites,* and *Lindstroemoceras*) was succeeded by the slender, slightly ovoid conch (as in *Ascoceras*) and finally by the nearly tubular adult conch (in *Glossoceras*). *Ascoceras* gave rise to *Aphragmites,* strongly annulated, and to *Glossoceras,* smooth and slender with restricted aperture.

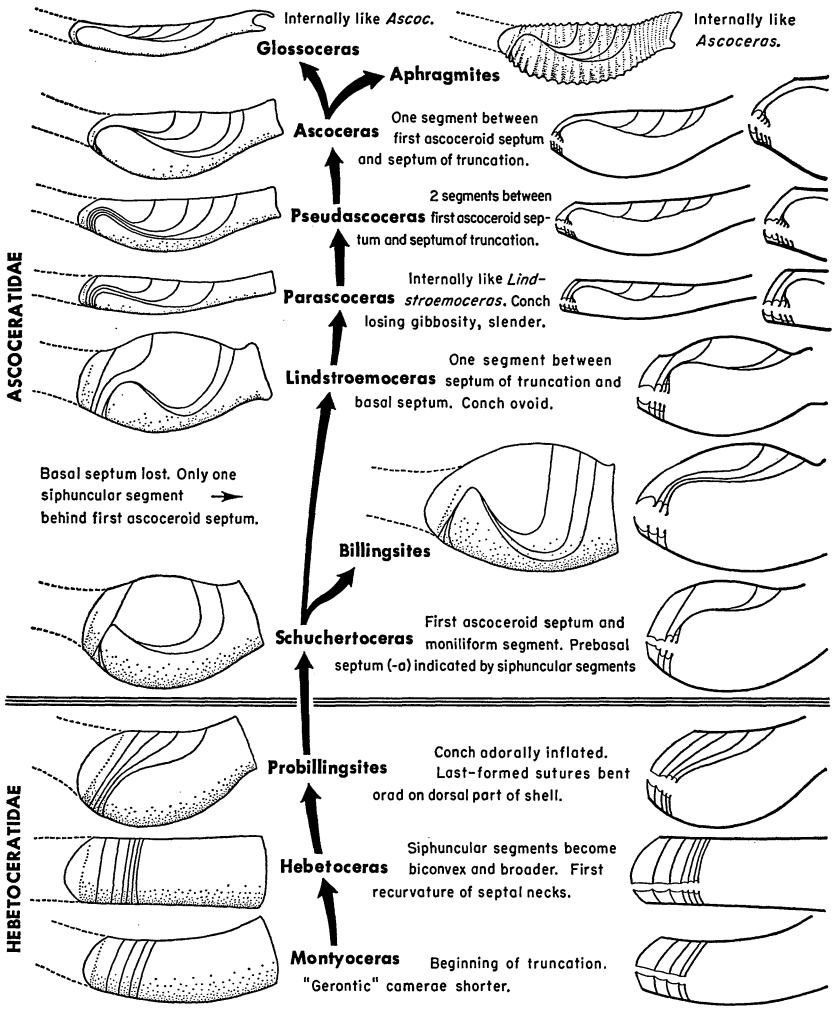

FIG. 2. Diagram showing evolutionary changes in the families Hebetoceratidae and Ascoceratidae of the order Ascoceratida. Genera are shown in stratigraphic sequence. Ovoid parts of the conch are shown at the left for each genus, with dashed lines indicating the adoral part of the cyrtoconic part. Vertical median sections are shown at the right for each genus. The section of *Probillingsites* is hypothetical. Figures are not drawn to scale. After Flower, 1941, Fig. 1.

In addition to the decrease in gibbosity, the ascoceratids display progressive loss of septa in the adapical end of the adult conch, next to the septum of truncation. Division of the siphuncle into segments between septa is thought to mark the former presence of a septum at the plane of constric-

tion (Flower, 1941, p. 530). *Schuchertoceras* retains two or three segments between the septum of truncation and the basal septum. *Lindstroemoceras* and *Parascoceras* have each only one in the same position (Fig. 2). In *Pseudascoceras* the basal septum is absent, but its former position is marked by siphuncular segments. *Ascoceras, Aphragmites,* and *Glossoceras* have each only one segment between the septum of truncation and the first ascoceroid septum. Although ovoid like *Schuchertoceras, Billingsites* quite suddenly, insofar as records are known, attained an internal organization comparable with that which by several small, progressive stages culminated in *Pseudascoceras* and *Ascoceras* in Middle Silurian.

A third evolutionary trend involves expansion of the siphuncular segments. This line of development began in the Hebetoceratidae. In *Montyoceras* all of the segments in the adult conch are planoconvex (Fig. 2). In *Hebetoceras* the adoral segments are biconvex. Unfortunately, the internal structures of *Probillingsites* have not been determined.

In the Ascoceratidae, *Schuchertoceras* has between the septum of truncation and the basal septum either (1) a planoconvex segment followed by two biconvex or (2) two biconvex segments; between the basal and the first ascoceroid septum it has a moniliform segment. Additional segments are moniliform and increase gradually in diameter. In *Lindstroemoceras* and *Parascoceras* the single segment behind the basal septum is biconvex, and all succeeding are moniliform. In *Pseudascoceras* there are two segments between the septum of truncation and the first ascoceroid septum, the first nearly planoconvex and the second moniliform. Supposedly, the constriction between them indicates the former position of the basal septum. *Ascoceras, Aphragmites,* and *Glossoceras* have all segments moniliform. *Billingsites* has no basal septum, and its siphuncular segments are like those of *Pseudascoceras* or *Ascoceras.*

By utilizing abbreviations, a simple and clear presentation of the reduction in septa and siphuncular segments can be made. The following are adopted here: *T,* septum of truncation; *B,* basal septum; *S,* undifferentiated septum; *A,* ascoceroid septum; *p,* planoconvex siphuncular segment; *b,* biconvex segment; and *m,* moniliform segment. Symbolically, the evolution in Hebetoceratidae and Ascoceratidae progressed:

T-p-S-p-S. . . .p-S - Montyoceras
T-p-S-p-S. . . .b-S - Hebetoceras
T-p-b-b-B-m-A. . .m-A - Schuchertoceras
T-b-b-B-m-A. . . . .m-A - Schuchertoceras
T-b-B-m-A. . .m-A - Lindstroemoceras, Parascoceras
T-b-m-A. . .m-A - Pseudascoceras
T-m-A. . . .m-A - Ascoceras, Aphragmites, Glossoceras

From *Schuchertoceras* was derived *Billingsites* with the following arrangements:

T-b-m-A. . .m-A - B. noquettensis, sp. nov.
T-m-A. . . .m-A - B. canadensis (Billings).

Genus *Billingsites* Hyatt

Type species.—By original designation of Hyatt, 1883, p. 278, *Ascoceras canadensis* Billings.

Differentiation of species.—Insofar as I have been able to compile from the scattered literature on *Billingsites,* nine species have been previously established (Fig. 3). *"Billingsites multicameratus?"* of Miller and Carrier (Fig. 4) seems also to be distinct, and the *"B.?* sp." of Strand may be different. Species include:

B. acutus Foerste, 1928*a*, p. 261, Pl. 28, Figs. 1–3; *B. bellicinctus* Miller, 1932*a*, pp. 242–43, Pl. 10, Figs. 3–5; *Ascoceras boreale* Parks, 1913, p. 192; *Ascoceras canadense* Billings, 1857, p. 310; *Ascoceras costulatum* Whiteaves, 1896, p. 394; *Ascoceras deforme* Eichwald, 1859, p. 1193, Pl. 49, Fig. 18; *B. elongatus* Foerste, 1928*a*, p. 260, Pl. 27, Figs. 1–2; *B. landerensis* Foerste, 1935, pp. 20–21, Pl. I, Figs. 4–5; *B. multicameratus* Miller, 1932*a*, pp. 243–44, Pl. 10, Figs. 6–8; *B. noquettensis,* sp. nov.; *"B. multicameratus?"* Miller and Carrier, 1942, p. 535, Fig. 1; and *"B.?* sp." Strand, 1933, pp. 55–56, Pl. 4, Figs. 5*a–b*.

Because, of the nine conchs of *Billingsites noquettensis* which have the dorsal surface of the steinkern preserved, all show remarkably similar arrangement of the sutures, I am convinced that the dorsal spacing of the ascoceroid sutures is a specific character. From descriptions and figures of other species of the genus, we see that in some it is the adapical sutures that are more closely spaced, whereas in others it is the adoral. It appears possible to distinguish the established species of *Billingsites* from the adult part of the conch, by comparing size of the conch, number of septa, spacing of sutures, and the position of suture reversals. In the following key, the species described by Miller and Carrier as *"Billingsites multicameratus?"* is regarded as a distinct species.

KEY TO SPECIES OF *Billingsites* BASED ON ADULT OVOID PART OF CONCH

1. Apex sharply acuminate, conch over 12 cm long ..... *B. acutus*
   Apex rounded, conch less than 12 cm long 2
2. Conch over 8 cm long ..... *B. costulatus*
   Conch less than 8 cm long 3
3. Three ascoceroid septa 4
   More than three ascoceroid septa 6
4. Nearly circular in cross section, height about ⅔ the length ..... *B. canadensis*
   Distinctly elliptical in cross section, height less than ⅔ the length 5

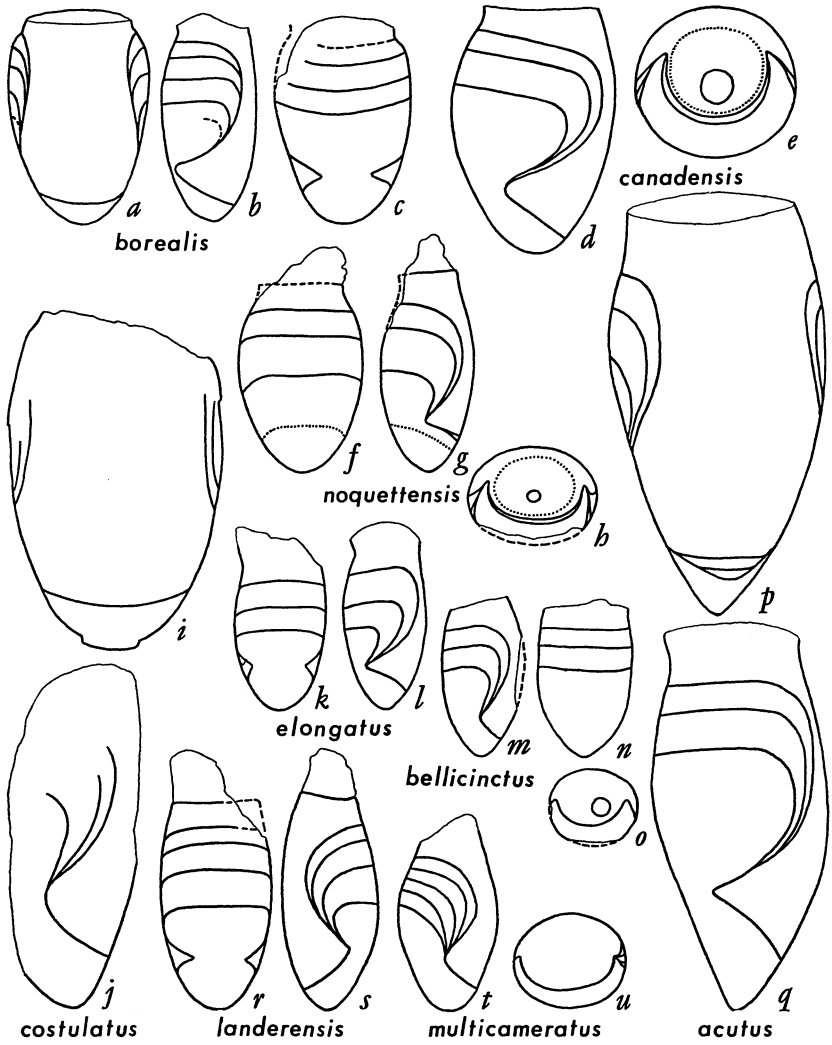

FIG. 3. Species of *Billingsites*. *a–c, B. borealis* (Parks), ventral, right, and dorsal views; in *b* the incomplete adapical suture indicated by a dashed line is probably an error in the retouched photograph from which the drawing was made, x ½. (After Foerste and Savage, 1927, Pl. 3, Figs. 4A–C). *d–e, B. canadensis* (Billings), right and apical views of different specimens, x ½. (After Foerste, 1928*a*, Pl. 40, Fig. 3, and Miller, 1932*b*, Pl. 4, Fig. 5). *f–h, B. noquettensis*, sp. nov., dorsal, right, and apical views, x ½. *i–j, B. costulatus* (Whiteaves), ventral and right views of different specimens, x ½. (After Whiteaves, 1897, Pl. 22, Fig. 1, and Foerste, 1929*b*, Pl. 13, Fig. 1A). *k–l, B. elongatus* Foerste, dorsal and right views, x ½. (After Foerste, 1928*a*, Pl. 27, Figs. 1–2). *m–o, B. bellicinctus* Miller, right, dorsal, and apical views, x ½. (After

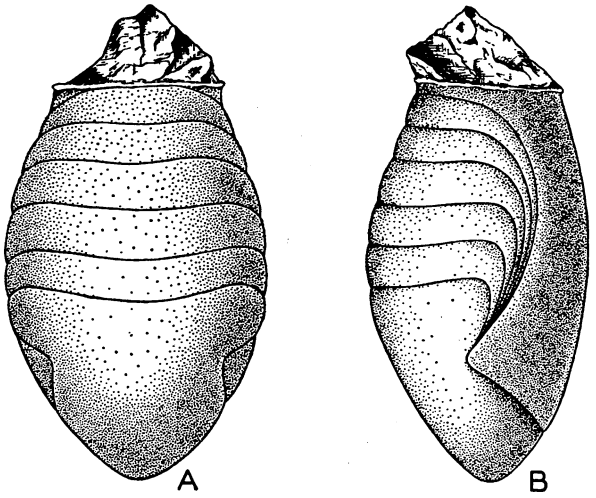

FIG. 4. *"Billingsites multicameratus* Miller?" as illustrated by Miller and Carrier, 1942, Fig. 1, x 1. This is probably a distinct species. A, dorsal view; B, right side.

5. Sutures at dorsal border about equally spaced ..... *B. bellicinctus*
   First and second sutures closer spaced ..... *B. elongatus*
   Second and third sutures closer spaced ..... *B. noquettensis*
6. Six ascoceroid septa, suture reversals dorsal ..... *"B. multicameratus?"**
   Five ascoceroid septa, suture reversals lateral ..... *B. multicameratus*
   Four ascoceroid septa, suture reversals lateral (?) ..... *B. deformis*
   Four ascoceroid septa, suture reversals dorsal 7
7. Greatest width near aperture, first suture crossing dorsal border in adoral half of conch ..... *B. borealis*
   Greatest width nearly central, first suture crossing dorsal border in adapical half of conch ..... *B. landerensis*

* From Miller and Carrier, 1942, p. 535, Fig. 1.

KEY TO SPECIES OF *Billingsites* WITH FOUR ASCOCEROID SEPTA

1. First suture crossing dorsal border in adapical half of conch, extending less than 3 cm from apex ..... *B. landerensis*
   First suture crossing dorsal border in adoral half of conch, extending more than 4 cm from apex 2
2. At dorsal border, sutures about equally spaced ..... *B. deformis*
   At dorsal border, adoral sutures closest spaced ..... *B. borealis*

Miller, 1932*a*, Pl. 10, Figs. 3–5). p–q, *B. acutus* Foerste, ventral and right views, x ⅓. (After Foerste, 1928*a*, Pl. 28, Figs. 2–3). *r–s, B. landerensis* Foerste, dorsal and left views, x ½. (After Foerste, 1935, Pl. 1, Figs. 4–5). *t–u, B. multicameratus* Miller, right and apical views, x ½. (After Miller, 1932*a*, Pl. 10, Figs. 7–8). Dashed lines indicate restored outlines; fine lines, the outline of the specimen but not the surface of the steinkern; and dotted lines, the cicatrix. Magnifications only approximate.

Some of the measurements that have been given for species of *Billingsites* are assembled in Table I. A clearer comparison of species can be had from Table II, in which the measurements have been reduced to proportions based on the distance from the apex to the dorsal limit of the adoral suture. The latter was selected as the most accurate parameter present in most specimens.

Billingsites noquettensis, sp. nov.

(Pl. I, Figs. 1–15; Pl. II, Figs. 1–9)

Billingsites newberryi noquettensis, Hussey, 1926, p. 182, Pl. 8, Figs. 10–12.
Billingsites newberryi noquettensis Foerste, Hussey, 1950, p. 20.
Billingsites newberryi Billings, Hussey, 1952, p. 51.

Adult conch.—Elongate ovoid, of two types. First, slightly larger, dorsoventrally depressed and elliptical in cross section, about 4.5 cm long, 2.9 cm wide, and 2.1 cm high; may be male. Second, slightly smaller, nearly circular in cross section, apically more acuminate, about 4.0 cm long, 2.4 cm wide, and 2.4 cm high; may be female. Holotype (Pl. I, Figs. 1–3) and most paratypes of first type. Three paratypes, two of them illustrated (Pl. I, Figs. 4–5; Pl. II, Figs. 3–9), of second type.

Three ascoceroid septa. Suture reversals lateral, not sharply bent. First ascoceroid suture crossing dorsal border about midway between apex and aperture, second about midway between the first and the aperture, and the third slightly more than half way from the second to the aperture; distance between first and second sutures almost twice that between second and third. Second and third sutures confluent about 1 cm adoral to the suture reversal, continuing adapically as one suture to junction with first suture at or near the suture reversal; thence, all three ascoceroid sutures confluent about one-third to one-half the distance to the ventral border; at the ventral border, the first and second sutures about .15 cm apart, second and third less than .10 cm apart. Between the junctions below the suture reversals, the first and second ascoceroid sutures outlining a much larger narrow crescentic area of the ventral surface than the second and third sutures (Pl. I, Figs. 1, 7, 15). Adorally from the suture reversal, the saddle formed by the first ascoceroid suture extending ventrally less than mid-height; saddle formed by third suture extending ventrally about four-fifths the distance from the dorsal to the ventral border (Pl. I, Fig. 3; Pl. II, Fig. 4). Ascoceroid sutures nearly straight as seen in dorsal view (Pl. I, Fig. 2).

Cicatrix of attachment indistinct in most specimens. In conchs of first type, elliptical in apical view, crossing ventral border about 0.3 cm and dorsal border about 1.0 cm ahead of the apex, subparallel to adapical sec-

TABLE I

MEASUREMENTS OF SPECIES OF *Billingsites*, ASSEMBLED FROM DESCRIPTIONS AND ILLUSTRATIONS*

Species	Length	Height	Width	Apex To Adoral Limit of Suture						Source
				1	2	3	4	5	6	
acutus	140	64	76	97	(109)	121	..	..	..	Foerste, 1928*a*, p. 261, Pl. 28, Figs. 1–3.
bellicinctus	[40]	21	25	26	31½	37	..	..	..	Miller, 1932*a*, pp. 242–43
borealis		34	55	46	53	59	62	..	..	Parks, 1915, p. 32.
borealis	(52)	25	36	(30)	(37)	(43)	(48)	..	..	Foerste and Savage, 1927, p. 30, Pl. 3, Figs. 4A–C.
canadensis	[55]	42	49	..	..	..	..	..	..	Foerste, 1928*a*, p. 260
canadensis	65	42	46	..	..	..	..	..	..	*Ibid.*, p. 260.
canadensis	(61)	..	(41½)	(42)	(50½)	(55½)	..	..	..	*Ibid.*, Pl. 40, Fig. 3.
canadensis	[56½]	(39½)	(46½)	(44½)	(53½)		..	..	..	Foerste, 1928*b*, Pl. 1, Figs. 1A–B.
canadensis	..	..	(42½)	(40)	(48)	(53)	..	..	..	*Ibid.*, Fig. 2.
costulatus	83	34	56	57	68	74	..	..	..	Foerste, 1929*b*, pp. 157–58
deformis	71	38½	47	(49½)	(54)	(58)	(62)	..	..	Eichwald, 1859, p. 1193, Pl. 49, Fig. 18.
elongatus	39	21	24	20½	26	35	..	..	..	Foerste, 1928*a*, p. 260.
landerensis	56	25	29	(27)	(36½)	(43)	(47½)	..	..	Foerste, 1935, pp. 20–21, Pl. 1, Fig. 5.
multicameratus	..	27	31½	32	35½	39	42½	46	..	Miller, 1932*a*, pp. 243–44.
"multicameratus?"	(53)	28	35	(23½)	(29½)	(36)	(42)	(47)	(51)	Miller and Carrier, 1942, p. 535, Fig. 1.
noquettensis	47½	21½	30½	23	33½	39½	..	..	..	Holotype

* Figures in brackets represent obviously incomplete measurements; those in parentheses represent measurements taken from figures. All measurements in millimeters.

TABLE II

PROPORTIONS OF SPECIES OF *Billingsites* COMPARED TO DISTANCE FROM APEX TO DORSAL LIMIT OF ADORAL SUTURE*

Species	Length	Height	Width	A–1†	Distance Between Sutures					Source
					1–2	2–3	3–4	4–5	5–6	
acutus	1.16	.53	.63	.80	.10	.10	..	..	..	Foerste, 1928*a*.
bellicinctus	[1.08]	.57	.68	.70	.15	.15	..	..	..	Miller, 1932*a*.
borealis		.55	.89	.74	.11	.10	.05	..	..	Parks, 1915.
canadensis	(1.12)	(.73)	.80	.76	.15	.09	..	..	..	Foerste, 1928*b*, Pl. 1, Fig. 2.
costulatus	1.12	.46	.76	.77	.15	.08	..	..	..	Foerste, 1929*b*.
deformis	1.14	.62	.76	.80	.07	.06	.06	..	..	Eichwald, 1859.
elongatus	1.12	.60	.69	.59	.16	.26	..	..	..	Foerste, 1928*a*.
landerensis	1.20	.53	.61	.57	.20	.14	.09	..	..	Foerste, 1935.
multicameratus	...	.59	.68	.70	.05	.08	.08	.08	..	Miller, 1932*a*.
"multi-cameratus?"	1.04	.55	.69	.46	.12	.13	.12	.10	.08	Miller and Carrier, 1942.
noquettensis	1.20	.54	.77	.58	.27	.15	..	..	..	Holotype.

* Figures in brackets represent obviously incomplete measurements; those in parentheses represent interpolations from other specimens.
† Distance from apex to adoral limit of first ascoceroid suture.

tion of first ascoceroid suture. Adoral mold of septum of truncation completely confluent with steinkern of outer wall in most specimens, slightly produced adapically in others.

Groove subparallel to adapical part of third ascoceroid suture, confluent with ascoceroid suture at about mid-length (Pl. I, Figs. 9, 14, 15; Pl. II, Figs. 1–2), thought to represent posterior ventral aponeurotic band. Second groove adoral and subparallel to it, also confluent with third ascoceroid suture at about mid-length (Pl. II, Fig. 2), thought to represent anterior ventral aponeurotic band.

Siphuncle large, ventrally constricted between septum of truncation and first ascoceroid septum (Pl. II, Fig. 9), about .27 cm in dorsoventral diameter in the adoral segment and about .22 cm at the constriction. Dorsally, the septal neck of the first ascoceroid septum distinctly recumbent. Apical end of siphuncle closed by an even, adapically convex layer of dense material (Pl. II, Fig. 9).

Septa very thin, only about .005 cm. In longitudinal section, ascoceroid septa not recurved ventrally, so that living chamber has no constriction. First septum only slightly sigmoid. Second and third septa fused just below dorsal limit of first septum, continuing adapically as one septum. Fused septum nearly tangent to first ascoceroid septum, but not quite in contact with it (Pl. II. Figs. 8–9).

Anterior camera divided into two curved, crescentic wedges, a large one dorsal and adoral and a small one ventral and adapical. Middle camera greatly constricted, only .01 cm wide a short distance above the siphuncle. In cross sections adoral to the siphuncle, camerae expressed as dorsal crescents.

Aperture elliptical, horizontally elongate (Pl. I, Figs. 1, 3), apparently at the terminus of a very gently curved neck.

One specimen, UMMP No. 37813, partly encase by a layer 0.1 cm thick (Pl. I, Fig. 9), thought to be replacement of the outer wall.

Cyrtocone.—Only steinkern of adoral section, about 3.2 cm long, known. Diameter apparently increasing regularly except for adoral margin; margin flared to join adult ovoid part of conch smoothly, making exact adoral edge of cyrtocone difficult to establish while still attached to adult part. Thirteen thin septa present in adoral 3.2 cm section of cyrtocone, the adoral three septa spaced within 0.2 cm and the others nearly equally spaced. Septum of truncation on adult part projecting back 0.75 cm into cyrtocone, showing no sutures on its surface. Crowded adoral septa of cyrtocone assumed to be subparallel to septum of truncation, the adapical convexity of cyrtoconic septa increasing from septum to septum, culminating in the strongly convex septum of truncation.

Remarks.—Billingsites noquettensis is in a different stage of evolutionary development than *B. canadensis,* with two segments between the septum of truncation and the first ascoceroid septum instead of one. Flower stated in 1941 (pp. 531–32): "No *Billingsites* having two segments is known; should one be found, the erection of a new genus for its reception might be justified. We have no assurance, however, that this condition does not exist in some known species now placed in *Billingsites.*" Of all the species previously described in the genus, still only one has been sectioned for siphuncular development, *B. canadensis* (see Fig. 2). Although good reason can be found to make the Ogontz specimens the type species of a new genus, in line with Flower's suggestion, such action would only introduce confusion at this time; until the internal organization of all species now included in *Billingsites* has been studied, creation of a new genus on the organization of one is superfluous.

The presence of two forms, one depressed and the other circular in cross section, has been interpreted as dimorphism. Specimens of each type do not seem to have any distortion of the sutures, so that the shape in cross section does not appear to be a product of fossilization. The living *Nautilus* exhibits dimorphism in the form of the apertural region, which is broader in the male to accommodate the bulky accessory sex organs, the spadix and antispadix. Nothing is known, of course, about the relative volumes of accessory sex organs in males and females of ascoceratid cephalopods. In the absence of evidence to the contrary, I have assumed that the male required greater space in the living chamber, as does the male of *Nautilus.* Flower (1945, pp. 184–85) discussed the possibilities of dimorphism in Ordovician *Probillingsites* and *Schuchertoceras,* but did not confirm its presence.

The new species can be easily distinguished from *B. acutus* and *B. costulatus* by its much smaller adult conch; from *B. canadensis* by its smaller height/length ratio; from *B. multicameratus, B. deformis, B. borealis, B. landerensis,* and the species called *"B. multicameratus?"* by Miller and Carrier by having only three ascoceroid septa; and from *B. bellicinctus* and *B. elongatus* by the closer spacing of its second and third ascoceroid sutures at the dorsal border.

The name suggested by Foerste many years ago and used as *nomen nudum* by Hussey, *noquettensis,* is based on the occurrence of the only known specimens on Stonington Peninsula within sight of Little Bay de Noc, formerly known as Bay de Noquette.

Types.—Holotype, UMMP No. 9831, the steinkern of an adult conch (presumed male). Illustrated paratypes: UMMP No. 37813, the steinkerns of adult part (presumed male) and adoral section of cyrtocone, found at-

tached and later separated; UMMP Nos. 43914 and 43917, the steinkerns of two adult conchs (presumed females); and UMMP Nos. 43915 and 43916, the steinkerns of two adult conchs (presumed males). Paratypes not illustrated: UMMP Nos. 43918–43921, steinkerns of four adult conchs (presumed males) and UMMP No. 43931, steinkern of adult conch (presumed female).

CEPHALOPOD BUOYANCY

Before attempting a restoration of *Billingsites noquettensis* and speculating on its life habits, let us examine some of the pertinent relationships of body and shell in *Nautilus,* the only surviving genus of the nautiloids.

Living Nautilus.—According to Stenzel (1952, p. H19; 1957, p. 1135) and others, *Nautilus* is a rapid swimmer. For practical purposes, swimming is its sole means of locomotion. The tentacles are adapted for feeding, not for crawling. The streamlined shell moves backward through the water, jet-propelled by water forcibly ejected through the hyponome. Air enclosed in the camerae of the phragmocone acts as a buoy. As Stenzel says (1952, p. H18): "*Nautilus* can no more turn over than a balloon can float with the gondola on top."

The camerae behind the living chamber are partitioned from one another and from the body by septa and from the tubiform backward extension of the mantle, the siphon, by the siphuncle, made up of septal necks and connecting rings. A connecting ring is lined with conchiolin and coated with a layer of calcareous spicules in a porous conchiolin matrix. In contrast, the septa and septal necks are composed of a thin conchiolin membrane and a thick nacreous layer of aragonite, built up as successive films. In life, the camerae are filled with air rich in nitrogen. For this reason, they have been called "air chambers," "loges aériennes," and "Luftkammern."

The manner in which cameral gas is formed bears directly upon the problem of buoyancy in fossil cephalopods. Until *Nautilus* attains the adult form, the shell muscles grow with the animal and migrate successively forward, pulling the body along in the living chamber. Thus a space is left between the last septum and the rear of the visceral sac, which gradually fills with gas, presumably liberated by arteries in the mantle (Stenzel, 1952, p. H17). When a certain volume of air space is attained, the mantle covering the visceral sac secretes a thin membrane of conchiolin. On this, in thin films, the nacre is deposited. This completes the formation of a new septum. By gradual growth, the siphon keeps pace with the movement of the body, and secretes its connecting ring between the new septal neck and the previous one.

"Because the septum is secreted by the septal face of the mantle, its shape exactly conforms to this face," according to Stenzel (1952, p. H17). But Griffin (1900, p. 105) has observed that ". . . the body wall is here so thin that the viscera can easily be distinguished through it." It seems odd that such a soft, thin mantle wall can form successive septa that are each smoothly convex adapical. The regularity of form, it seems to me, can be explained only as the result of lower pressure in the preseptal space than in the body. Hence, the body wall would be bowed out backward by suction from the preseptal cavity and, as a natural response, assume a regularly convex shape.

Among other characteristics, maturity in *Nautilus* is marked by crowding of the last two or three septa, greater thickness of the last septum, and thickening of the shell margin (around the aperture), as listed by Willey (1902, p. 748) and Stenzel (1952, p. H16).

Two controversies concerning hydrostatic adjustment have not been clearly decided by biological observations. The first: does pressure change within the camerae, and if so how? *Nautilus* has been reported trapped at depths of 450 to 700 meters (Dean, 1901, p. 821), but it has also been taken alive, by divers, from water only a few meters deep. Hence, the animal is equipped to withstand radical changes in external pressure. Willey (1902, p. 747) stated: "It is, I am convinced, an error to suppose that variations of pressure of the air in the chambers enable *Nautilus* to rise or sink as the case may be. The air simply renders the shell buoyant once for all." It seems likely, however, that the cephalopod could somehow adjust the internal pressure within the camerae to conform with external pressure on the conch. Only the siphon connects the body with the older chambers, traversing through the septal necks and connecting rings. Pia (1923, p. 59) and Schmidt (1925, p. 314) have suggested that, despite statements to the contrary, the structure of the connecting rings probably presented no hindrance to passage of gas. Stenzel (1952, p. H12) concluded: "Possibly the blood in the siphuncle [siphon] gradually equalizes and adjusts the gas pressure in the air chambers to conform with the hydrostatic pressure of the water surrounding the animal."

Inasmuch as equilibrium is a delicate balance of gas/body volumes, it is possible that expansion of the siphon increased the pressure inside the camerae, decreased the gas volume, and initiated descent in the water. Schmidt (1925, p. 313) wrote: "Man hat zeitweise geglaubt . . ., der Sipho sei dehnbar, das Tier besitze die Fähigkeit, ihn mit der Flüssigkeit der Leibeshöhle vollzupumpen, so dass er stark ausgedehnt wird, die Luft der Kammern komprimiert, so ihren Auftrieb verringert und ein Sinken des

Tieres herbeiführt." Thus, the adjustment of buoyancy and internal pressure may be controlled simultaneously.

The second controversy, which has led to unbounded defense of unfounded hypotheses: does the adult animal possess a small volume of preseptal gas, which can act as a swim bladder to raise or lower it in the water? Meigen (1870, p. 28) reported that a *Nautilus* with a living chamber of 1300 cc had about 3 cc of preseptal gas. Schmidt (1925, p. 59) accepted this as a true condition in cephalopods and based some of his suppositions about ammonites on it, as did Tobein (1949, pp. 312, 316) in his work on ascoceratids. Teichert (1933, p. 192) accepted the idea of preseptal gas, but (p. 193) estimated its effect to be insignificant. Flower (1957, p. 837) and others have thought the report a myth, and proposed that pressure and volume accommodation could be accomplished by expansion and contraction of the body. Flower (1957, p. 835) said that the proposal of Meigen had been followed "unfortunately."

There is no question about the presence of preseptal gas in all stages of *Nautilus'* development before the adult stage is attained. In fact, the formation of new camerae would not be possible without the forward movement of the body and creation of a preseptal space. Possibly, there is also an adjustable gas space ahead of the final septum. Certainly, the question can be solved only by carefully examining living animals, and not by theoretical considerations.

General considerations.—"Most nautiloids adopted a pelagic existence in which buoyancy was a paramount consideration" (Easton, 1960, p. 418).

A brief mathematical treatment simplifies the discussion of buoyancy and shell thickness. Teichert (1933) presented a detailed analysis of the factors for orthocones, more detailed than is necessary here. He assumed the specific gravity of 1.03 for sea water, 1.08 for soft parts of the animal, and 2.6 for shell material. In view of the high percentage of aragonite in the shell, 2.7 seems a more realistic figure for specific gravity; Teichert's other values are adopted. In the following equations, these symbols are used:

B = buoyancy, the summation of forces acting on the cephalopod (gm),
G = volume of preseptal gas (cm^3),
L = internal volume of the living chamber (cm^3),
L' = volume of body (cm^3),
S = volume of shell material around the phragmocone and the living chamber (cm^3), and
P = volume of gas within the phragmocone (cm^3).

Buoyancy can be expressed as a relationship of weights or forces acting to lift (+) or depress (—) the cephalopod in water:

$$B = 1.03\ (L' + P + S + G) - 1.08\ L' - 2.7\ S$$
$$= 1.03\ (P + G) - .05\ L' - 1.67\ S.$$

At hydrostatic equilibrium, $B = 0$ and the shell material is

$$S = .617\ (P + G) - .030\ L'.$$

It may logically be assumed that the body will be about 1.25 L and that preseptal gas, if present, will occupy no more than one-fourth of the living chamber, that is,

$$L' = 1.25\ L \text{ and } G = .25\ L.$$

In that case, the maximum shell substance that would be supported at equilibrium (with preseptal gas present) would be

$$S_2 = .617\ P + .117\ L,$$

and the minimum shell substance (absence of any preseptal gas)

$$S_1 = .617\ P - .037\ L.$$

The effect of maximum preseptal gas in terms of shell volume is

$$S_2 - S_1 = .154\ L.$$

Thus, at most, preseptal gas could support enough shell material to fill about 15 per cent of the living chamber.

It may be borne in mind, from the original equation for buoyancy, that preseptal gas has exactly the same lifting force as a corresponding volume increase in the phragmocone.

To investigate the relationship of buoyancy to shell and body volumes, it is necessary to assume that in fossil shells the body protruded from the living chamber by one-fourth its volume. Any preseptal gas could, if proved to have existed, be accounted as an effective addition to the phragmocone. Hence, the cephalopod is considered to have consisted of shell, body, and phragmocone. If these are expressed as percentages of the total volume, then

$$S + L' + P = 100,$$
$$P = 100 - L' - S, \text{ and}$$
$$B = 1.03\ (100 - L' - S) - .05\ L' - 1.67\ S$$
$$= 103 - 1.08\ L' - 2.70\ S.$$

Buoyancy in this form has little significance. It is much better defined in terms of the reduced weight of the body only:

$$B' = B/.05\ L' = (103 - 1.08\ L' - 2.70\ S)/.05\ L'.$$

This permits comparison of the buoyancy of the cephalopod with that which it would have if the shell (and gas in the phragmocone) were absent. The living squid and cuttlefish would have, essentially, $B' = -1$. We may interpret $B' = -2$ to mean that the cephalopod in water became twice as heavy on account of the conch; $B' = -5$ would mean that the

animal was five times as heavy because of the conch, and presumably would need five times as much energy to swim; $B' = +2$ would mean that it was held at the surface by a force equal to twice its weight in water.

Calculations are simpler if the volume of shell is expressed in terms of the body volume and the buoyancy:

$$S = 38.15 - .40\ L' - .0185\ L'B'$$

Thus, if the body were 50 per cent of the total volume, the cephalopod would attain equilibrium ($B' = 0$) when the shell material amounted to

$$S = 38.15 - 20.00 = 18.15 \text{ per cent of the total volume.}$$

Values of B' have been plotted on a chart of body (L') vs. shell (S) in Figure 5.

The percentage of shell material can also be computed as a ratio of the thickness of the outer wall (computed to include the material in the septa and siphuncle) to the radius of the conch. This is particularly helpful in considerations of the orthoconic and cyrtoconic cephalopods. The volume of the conch with length l, shell thickness t, and radius R is

$$V_2 = \pi\ R^2\ l/3,$$

whereas the phragmocone and living chamber occupy

$$V_1 = \pi\ (R - t)^2\ l/3$$

and the shell material

$$S = V_2 - V_1 = \pi\ (2\ Rt - t^2)\ l/3.$$

However,

$$V_2 = 100 - L'/5$$

so that

$$\frac{S}{100 - L'/5} = \frac{2\ Rt - t^2.}{R^2}$$

From this formula, for each value of L' the amount of shell can be computed for various thicknesses of shell expressed in terms of the radius. In this way, values of shell in terms of radius were determined and entered in Figure 5 as vertical series of short marks.

FIG. 5. Chart of buoyancy as compared with that of the body only (B') plotted on percentages of body (L') vs. shell material (S). Vertical series of marks indicate the amount of shell material produced by an outer wall expressed in terms of the radius of the conch. The heavy line represents equilibrium, the dashed lines units of positive buoyancy, and the thin lines units of negative buoyancy. Certain points plotted on the chart are referred to in the text: A, *Nautilus,* both immature and adult; B–G, *Billingsites noquettensis* in several of the stages of development postulated in Table IV, B, stage K; C, stage B; D, stage D; E, stage L; F, stage I; and G, stage A. The computations are based on a hypothetical cephalopod in which the body is one-fourth larger than the living chamber.

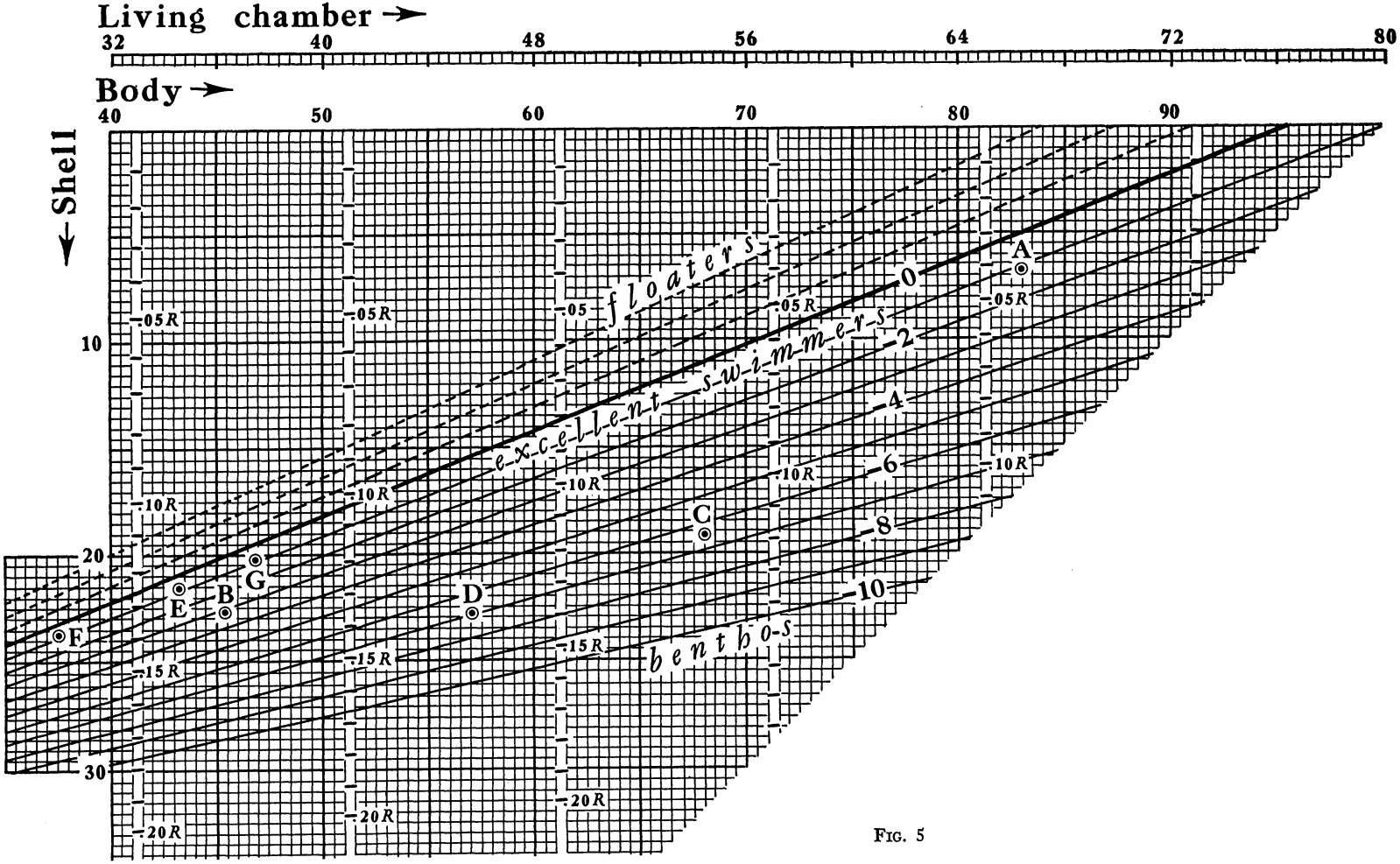
Living chamber →
32
40
48
56
64
72
80
Body →
40
50
60
70
80
90
← Shell
10
20
30
floaters
excellent swimmers
benthos
0
2
4
6
8
10
.05R
.10R
.15R
.20R
A
B
C
D
E
F
G

FIG. 5

The estimated body and shell values (82.9 and .041R) for living *Nautilus* are entered in Figure 5 as point A. These estimates are based on my measurements of two specimens of *Nautilus* in the Museum of Paleontology; the figure for the body percentage agrees very well with the report by Tobien (1949, p. 311) that the camerae occupy about 30 per cent of the internal volume. The buoyancy of *Nautilus* is about —1.1; that is to say, the animal weighs little more, if any, than it would with no conch, and can swim with no more expenditure of energy than the squid. Unfortunately, however, *Nautilus* is the only surviving shelled cephalopod. There are no others from which the limits of buoyancy and swimming ability can be deduced. It seems reasonable to believe that an animal with a buoyancy of —3 would be a poor swimmer, and that one with buoyancy of —10 would scarcely be able to lift itself off the bottom, even for a brief interval. From Figure 5 it is readily apparent that for a given percentage of body the buoyancy changes drastically with the addition or deletion of shell material amounting to only a few hundredths of the radius, and that as the percentage of body decreases (and the percentage of phragmocone increases accordingly) the buoyancy becomes more critically dependent upon the percentage of shell material.

The chart in Figure 5 enables us to determine quickly the effect of preseptal gas on buoyancy. Suppose the proportion of body-shell-gas (phragmocone) in the absence of preseptal gas is 70–15–15; then with addition of preseptal gas equal to $L'/5$ the proportion changes to 61.4–13.2–25.4, the size of body and quantity of shell material remaining constant. The addition of preseptal gas, in this example, has changed the buoyancy from —3.7 to +0.2. This means that preseptal gas can change a poor swimmer to a floating animal. Hence, the presence or absence of preseptal gas has a profound effect on the ecology of the cephalopod.

This conclusion differs from that of Teichert (1933, p. 193), who concluded that the argument over existence of preseptal gas was unimportant because its lifting power was very little of the whole. Insofar as the amount of shell material that could be supported by the addition of preseptal gas is concerned, Teichert is correct that it matters little; but in the matter of buoyancy, if the quantity of gas could be regulated it would provide the sufficient change in total specific gravity to upset the hydrostatic balance, permitting the cephalopod to rise or sink, as suggested by Tobien (1949, p. 312).

As pointed out above, the convex shape of the adapical end of the body at the time of septal formation points to lower pressure in the preseptal space than within the body. Possibly, when the animal extends the tentacles from the body it puts greater tension on the adapical wall and

therewith increases the preseptal space; this would add to the buoyancy and permit the animal to swim with greater efficiency. Conversely, when the animal retracts the tentacles and withdraws into the living chamber it may relax the tension on the adapical wall, decreasing the preseptal space and permitting the animal to sink more rapidly.

From time to time, suggestions have been presented that fossil cephalopods may have augmented calcareous deposits with fluid in the camerae. Dunbar (1924, p. 207) stated that: "if fluid ballast had been employed, no tangible evidence of the same might be preserved. Such evidently was the case for those straight shells like *Orthoceras* which permanently retained a horizontal orientation without change of shell form." In view of the wide range in buoyancy that can be effected by a small change in shell thickness or by creation of preseptal gas, as revealed in the computations above, it hardly seems necessary to postulate fluid ballast to explain buoyancy in any of the orthoconic or cyrtoconic forms.

Nautilus has approximately the same buoyancy when very small, half-grown, and adult, based on reported measurements of living chamber and phragmocone. Undoubtedly, many fossil cephalopods similarly retained the same, or nearly the same, proportions of body, shell, and gas in the phragmocone. Therefore, the same general relations of parts must have been maintained throughout the ontogeny, and the conch may be looked upon as an accumulation of successfully balanced increments. For a cephalopod to have retained nearly constant buoyancy throughout its lifetime, the thickness of shell material must have been a fixed proportion of the diameter in each camera. Hence, our assumption that shell material can be measured as a ratio of thickness of outer wall to radius seems to be valid.

There are certain other ways in which buoyancy can be affected. Buoyancy could be decreased by (1) closer spacing of septa, (2) thicker septa, (3) cameral deposits, (4) intrasiphonal deposits, (5) increasing in proportion of the body protruding from the aperture, or (6) thicker outer wall, as around the adult aperture.

The attitude of the conch in the water is much more difficult to estimate than the buoyancy. The center of gravity, determined by the distribution of body, shell, and gas, comes to rest below the center of buoyancy, determined by the distribution of displaced water (hence, directly by the shape of the conch). These centers are established as the points about which the moments of force are balanced. For most fossil forms, the measurements of shell, phragmocone, and living chamber are not sufficiently accurate to yield reliable estimates of the centers of gravity and buoyancy. Even if these could be measured at close intervals throughout the conch, there is no way to determine the size of the body exactly. At best, only rough estimates of the attitude of the conch can be made.

Several hypotheses on cephalopod attitude stem from illogical assumptions. Some envisage a phragmocone encased in weightless shell and held below the surface of the sea by a ponderous body in a leaden living chamber; they suppose all conic forms were vertical, apex uppermost. Others claim that each new chamber is more buoyant than the preceding one, neglecting the fact that it is ensheathed by a thicker wall and must help to support a larger mass of soft parts. If this were true for a young cephalopod in equilibrium, one may only conclude that addition of the next chamber hoisted the animal to the surface and that further additions served to elevate more and more of the conch above the water. For each kind of conch, one must regard the ontogenetic sequence. Each camera has its own buoyancy, established by the composition and amounts of shell and gas, which is added to and integrated with the buoyancies of the preceding camerae and the increase in the size of the living chamber. The conch becomes a series of firmly joined increments of buoyancy. Furthermore, it must be borne in mind that cumulative ontogenetic increases in buoyancy, especially those resulting in change from nektonic to planktonic existence, would have to be accompanied by adaptations in the body to secure food in the new environment. Probably, some cephalopods floated as adults, as has been assumed, but they were the exceptional forms and relatively few made the transition from scavenger to filter feeder.

Billingsites' MODE OF LIFE

The ascoceratids have evoked nearly as much writing on their supposed life habits as on their preserved structures. This is to be expected for animals that developed the peculiar characteristic of truncation, suddenly casting off and abandoning part of the shell which previously had served a useful function. One day the cephalopod lived with the cyrtocone, the next day without it. No period of gradual adjustment was possible. Irreversibly, the ascoceratid launched into a different way of living, and, as an individual, it was successful. As Schindewolf expressed it (1950, p. 142 [his italics]), "Auch diese bezeichnenden Sondermerkmale der Ascoceran sind offenbar *sprunghaft* entstanden, wenigstens sind zurzeit *keinerlei Übergänge* bekannt."

Although none of the published works concern the paleoecology of *Billingsites* directly, they express the current concepts on the peculiar group of the ascoceratids.

Previous work on ascoceratids.—Truncation is such a climactic act that one might expect, with minor variations, agreement on the change it wrought in the life habits of the cephalopods. Instead, theories are diametrically opposed. One group believes it signals the beginning of benthonic

existence by loss of the buoyant phragmocone, whereas the other group looks upon it as the introduction to free swimming by removal of an unwieldy and impeding section of the conch.

Dacqué (1921, p. 110) said, "Man kann daraus schliessen, dass diese reduzierte Form zum Bodenbewohnen überging, während die langgestreckte pelagisch lebte, wie ein *Orthoceras*." And Abel (1924, p. 205) wrote, ". . . *Ascoceras* und seine Verwandten in der Jugend eine nektonische, im Alter dagegen eine rein benthonische Lebensweise führten."

Pia (1923, p. 61) reached a very different conclusion. He thought that after truncation *Ascoceras* would be an excellent swimmer with the body horizontal, like *Octopus*.

Dunbar (1924, p. 198) referred to the ideal balance in coiled forms, and went on to say, "Balance was apparently attained in a different manner by the enigmatic Mixochoanites such as *Ascoceras*. After starting their growth with the cameration posterior to the body and a curving tip to the shell, these cephalopods later begin to form incomplete 'saddle-like' septa, cutting off a series of chambers along the dorsal side of the shell . . . Their form in such species as *Ascoceras bohemicus* should give an almost ideal balance to the shell, removing the stimulus to coiling." And on page 206 he added that after truncation the broken end was "then patched by a characteristic plug, which was secreted from without, apparently by means of specialized arms, such as those . . . in *Argonauta* . . ."

Miller (1932*b*, pp. 58–59) concluded his scholarly work on the Mixochoanites (now Ascoceratida) with an interpretation of the mode of life of the adult cephalopods. Because this paper has strongly influenced subsequent opinions, it is here quoted extensively:

> . . . one can not help but wonder how many of the cyrtoconic forms controlled the direction of their progression during backward propulsion. Therefore, it must have been distinctly advantageous to break off the earlier stages of the phragmocone and thus remove much of the impediment to rapid and straight progression. Such truncation, however, necessitated the development of a few large camerae or gas chambers next to the living chamber to serve as buoys, and this will perhaps account for the globular form assumed by the early mixochoanites . . . These early forms . . . apparently had two serious handicaps: first, when the animal came to rest its conch must naturally have assumed a vertical position with the aperture down . . . and, second, its globular form must have retarded its passage through the water. The first of these handicaps was surmounted by the development of long, deep dorsal saddles in the adoral septa (the ones that were retained after truncation), so that the phragmocone (buoy) was extended all along the dorsal part of the conch and the weight of the animal's body was distributed all along the ventral. The second handicap was overcome by what superficially appears to be a reversal in evolution in that the conch tended to become long and narrow again, but this time it assumed a spindle-like or fusiform shape, which is particularly advantageous for subaqueous locomotion.

As already discussed, Teichert (1933) presented pertinent data on the general problem of cephalopod buoyancy, although he did not mention ascoceratids.

Flower (1941) in his excellent taxonomic study of the ascoceratids also concerned himself with their paleoecology. Of the evolution of the group, he said (p. 534): "In the elongation of the shell, extension of the aperture, and development of a compressed section, it is possible to see adaptive modifications . . . the compressed form and the elongation of the shell produce the most perfect approach to the ideal stream-line form found in the cephalopods. The animal moves in a reverse direction, being propelled by the force of the hyponome. As a consequence the oblique septum of truncation, together with the shell wall, forms an excellent blunt nose, beyond which the shell soon attains its maximum diameter. Then, by reason of the produced aperture, the shell tapers more gradually to its termination. The outline is completed by the addition of the soft parts, consisting of a protruding head equipped with long tentacles." He further suggested that the arms in the ascoceratids were probably long, few, and "might even have had some finlike developments." On the subject of the truncated siphuncle, Flower commented (p. 535), "The septa serve as excellent partitions already in place, and the closure of the apex of the shell requires only the secretion of material by the apical end of the siphuncle, an organ capable of building much more elaborate structures . . ." This is in sharp contradistinction to the suggestions of Barrande (1877, pp. 303, 305), Abel (1924, pp. 186–87), and others that the truncated end of the siphuncle was closed by deposits laid down by long arms reaching back over the conch, secreting calcium carbonate much in the manner of the arms in living *Argonauta.*

After reviewing the ascoceratids, Flower concluded that these cephalopods represented an example of lipopalingenesis, with ontogenetic stages rapidly removed during evolution; he said (p. 538): "Possibly it had to do with shortening the period of immaturity . . ." He also stated (p. 538) that "the ascoceroid could not attain effective motility until the mature conch was completed."

The most recent work of significance is that of Tobien (1949), who concluded that *Glossoceras,* with its elongate, sleek, torpedo-shaped, laterally compressed form, was especially adapted for active swimming by the hyponome, and (p. 321) that benthonic existence of ascoceratids was improbable. He studied the internal organization in *Ascoceras,* finding that the gas chambers occupied 28 to 36 per cent, averaging 33 per cent, of the total conch. He investigated the attitude of the shell by means of three-dimensional models. Tobien was an advocate of preseptal gas, supposing (p. 312) that it aided in lifting and lowering the conch and (p. 314) that

evidence for its existence was to be found in the supernumerary septa formed in certain specimens. He stated (p. 313): "Man kann . . . ebenfalls in Analogie zum rezenten *Nautilus* und seinen ausgestorbenen Verwandten . . . eine permanent vorhandene Gasmenge, welche nach der Bildung des vordersten sigmoiden Septums abgeschieden wurde und sich zwischen diesem und der Wand des Weichkörpers befunden hat, voraussetzen."

Stages of development.—Reasonable assessments of cephalopod adaptation must include the continuity of the conch. Every conch contains, so to speak, a collection of past conchs, in each of which the animal spent part of its life. One stage cannot be examined independently. This is particularly true for the ascoceratids with their diverse youthful and mature forms. Thus, although *Billingsites noquettensis* was very different as a cyrtocone, after formation of the adult ovoid part of the conch, and after final truncation, and although it obviously altered its buoyancy several times, the same animal maintained itself through the radical changes in shape.

Billingsites noquettensis undoubtedly began life as a small cyrtocone, not very strongly curved, if we may judge from the cyrtoconic sections known in Silurian ascoceratids. Easton (1960, p. 419) remarks that ". . . a cyrtocone is the most poorly designed conch to control during its movement through the water. If it were propelled rapidly it would tend to describe a series of loops; in fact, it would be no more controllable than a banana-shaped rocket." The curved shape did, however, offer one advantage over the orthoconic. The upward tilt of the phragmocone at the apical end effectively counteracted any tendency to "roll" (in the aeronautical sense of the word).

The only cyrtoconic section found is part of the paratype UMMP No. 37813. It is adapically incomplete, but shows certain features of the immature part of the conch. From the taper which it exhibits, we may adjudge that the complete cyrtocone was about 10 cm long. It expanded regularly until it approached the adult ovoid part, where it flared slightly outward.

In UMMP No. 37813 the steinkern of the adult part broke free, revealing that the septum of truncation is adapically subovoid, as in other specimens studied, and projects back into the adoral end of the cyrtocone by about 0.75 cm (compare Figs. 9–10 with Figs. 12–14 in Pl. I). Inasmuch as the septum of truncation shows no sutures on its surface, we may conclude that the crowded septa immediately adapical to it are also subovoid and nearly parallel.

The approach of maturity was recorded in the conch by the beginning of a very different part, which, for a time, was continuous with the cyrtocone. It was patently impossible for the septum of truncation to have preceded the adapical section of the outer wall of the ovoid part. As the latter

was being formed, the body of the cephalopod could increase by a given percentage without moving very far forward, due to the expanded living chamber. This seems to be the explanation for the close spacing of septa just behind the septum of truncation, three of which occur in less than 2 mm.

At the time in the ontogeny when the outer wall of the adult part was being laid down by the advancing mantle edge, the body occupied both the adoral section of the cyrtocone and the incomplete ovoid part of the conch. It is difficult to conceive that the mantle edge expanded in the advance of 2½ cm from 2 to 3 cm in greatest diameter, and in the next 2 cm contracted to less than 2 cm in diameter. Yet that must indeed have been the manner in which the outer wall of the adult conch was made. One cannot imagine that the ovoid adult body protruded naked from the neck of the cyrtocone prior to formation of the adult conch.

The thickness of the septum of truncation is not known. Nevertheless, there is no reason to doubt that it was about as thick as the outer wall, as it has been observed to be in Silurian ascoceratids. It constituted a rather sudden addition of weight, which must have strongly influenced the buoyancy. Until the secretion of the septum was complete, no preseptal gas space could form in advance of it to alleviate some of the burden. From the size of the adult body, determined from sections through the living chamber (see Table III), it seems improbable that even half of the ovoid wall was deposited before the septum of truncation. According to calculations of volume, the body at the time of completion of the cyrtocone could grow to nearly twice its size and fit into the adapical 2.5 cm of the adult part of the conch.

As soon as the work of secreting the septum of truncation was over, the adapical wall of the body was drawn forward to create a preseptal gas space. This restored some of the cephalopod's buoyancy by counterbalancing some of the thick septum of truncation. The first ascoceroid septum was undoubtedly formed before the outer wall attained the final aperture. A body nearly as large as the final adult form could be accommodated ahead of the first ascoceroid septum in the adapical 3.25 cm of the adult conch. Similarly, the second ascoceroid could have been laid down when the adult part was only 4.0 cm long without extruding the soft parts.

From UMMP No. 37813 we learn that this specimen formed the complete adult part, including all ascoceroid septa, prior to truncation of the adoral 3 cm of the cyrtocone. It is impossible without additional specimens at this stage to confirm whether this was a normal ontogenetic sequence. I am inclined to regard it as the rule for the species, as will be explained later in connection with buoyancy.

TABLE III

APPROXIMATIONS OF VOLUMES OF TOTAL CEPHALOPOD (V'), SHELL MATERIAL (S), PHRAGMOCONE (P), AND BODY (L') AND COMPUTATIONS FOR DETERMINING CENTERS OF BUOYANCY AND GRAVITY IN *Billingsites noquettensis*.

	Apex	Conch (Sections Spaced 0.5 cm Apart)								Aperture	Protruding Body		Total
	0	A	B	C	D	E	F	G	H	I	J	K	
Width (cm)	0.40	1.60	2.20	2.60	2.80	3.00	3.00	2.60	2.20	1.60			
Height (cm)	.27	1.07	1.47	1.73	1.87	2.00	2.00	1.73	1.47	1.07			
V' (cm^3)*	.37	1.21	1.91	2.47	2.78	3.00	2.63	1.91	1.21		1.00	.82	19.31
Area (cm^2)*	2.55	3.59	4.26	4.57	4.91	5.00	4.96	4.26	3.58				
Thickness of shell (cm)	.100	.100	.105	.110	.115	.120	.125	.130	.135				
S (cm^3)	.26	.36	.45	.50	.56	.60	.62	.55	.48				4.38
P (cm^3)†	.11	.75	1.05	1.10	1.11	1.00	.84	.20	.00				6.16
L' (cm^3)	.00	.10	.41	.87	1.11	1.40	1.17	1.16	.73		1.00	.82	8.77
Displaced water (gm)	.38	1.26	1.99	2.57	2.89	3.12	2.74	1.99	1.26		1.03	.84	
Distance from center of buoyancy (cm)‡	2.45	1.95	1.45	.95	.45	... .05	.55	1.05	1.55		2.05	2.55	
Moment around center of buoyancy	.93	2.46	2.89	2.44	1.30	... .31	1.51	2.09	1.95		2.11	2.14	
Total weight (gm)	.70	1.08	1.66	2.29	2.71	3.13	2.93	2.74	2.09		1.08	.89	
Distance from center of gravity (cm)§	2.58	2.08	1.58	1.08	.58	.08	... .42	.92	1.42		1.92	2.42	
Moment around center of gravity	1.81	2.25	2.62	2.47	1.57	.25	... 1.23	2.52	2.97		2.07	2.15	

* Volumes and areas of segments computed as for frustra of rectangular pyramids with equivalent volumes and areas.
† Estimated for each segment from median sections and steinkerns of specimens.
‡ Center of buoyancy established by trial at about 2.70 cm from apex.
§ Center of gravity established by trial at about 2.83 cm from apex, 0.13 cm adoral from the center of buoyancy.

The absence of the adapical section of the cyrtocone in UMMP No. 37813 suggests that *Billingsites noquettensis* may have performed subadult truncation. Such truncation is known in other cephalopods. In *"Orthoceras" truncatum,* for example, each adult had truncated some fifty times (Dunbar, 1924, p. 206). It is possible that in *Billingsites* the immature animal cast off small adapical segments, at once decreasing the buoyancy to a desirable condition and modifying the awkward cyrtoconic shape.

Several possible forms of *Billingsites noquettensis* are sketched in Fig. 6. Very young cephalopods (Fig. 6*a*) and the juvenile (Fig. 6*b*) with cyrtoconic conchs undoubtdly existed. The truncated juvenile (Fig. 6*c*) is unlikely from the standpoint of buoyancy; with much of the gas in the phragmocone lost by truncation, it would be many times heavier in water than the preceding stage with a complete cyrtocone. The subadult stage shown in Fig. 6*d* is modeled after UMMP No. 37813. The actual procedure of truncation is not known, so that the supposition that the deterioration of the conchiolin and solution of the aragonite permitted flooding of the cyrtoconic camerae before truncation (Fig. 6*e*) may be questioned. As pointed out above, the stage in which the first ascoceroid septum was deposited (Fig. 6*f*) probably did not yet have all of the outer wall. The final adult (Fig. 6*g*) is shown in what is thought to be the normal swimming position.

The question of when the adapical section of the cyrtocone may have been truncated can be more logically answered after the buoyancies of the possible forms have been computed. It is discussed below.

There remains the problem of preseptal gas in the adult. Two specimens (Pl. I, Figs. 12–15; Pl. II, Figs. 1–2) show grooves that are interpreted as posterior ventral aponeurotic bands separated from the last ascoceroid septum. If this interpretation is correct, then the adult had preseptal gas space amounting to perhaps 1 cm^3. Possibly, not all ascoceratids had preseptal gas as adults; Tobien (1949) found what seems to be a posterior ventral aponeurotic band next to the last septum in *Ascoceras*.

Function of truncation.—More intriguing than the formation of an ovoid part as the terminus of an earlier cyrtoconic conch is the universal procedure of truncation among ascoceratids, casting off finally all of the cyrtocone. Insofar as the history of the ascoceratids has been worked out by Flower (1941) and others, truncation was established in these cephalopods before they developed ovoid terminal parts of the conch (see Fig. 2). Furthermore, such species as *"Orthoceras" truncatum,* the outstanding example of multiple truncation, never developed ovoid adult conchs.

Truncation may be assumed to have served a critical need of the animal. As Dunbar observed (1924, p. 206), ". . . this truncation of the air cham-

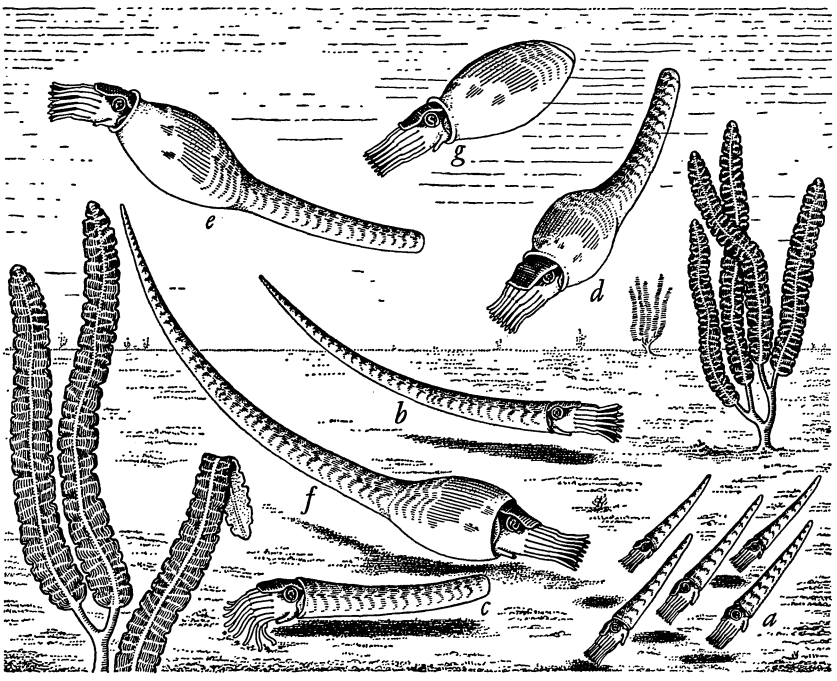

FIG. 6. Reconstruction of Upper Ordovician sea bottom showing hypothetical ontogenetic stages of *Billingsites noquettensis,* sp. nov. *a,* young cephalopods in which the siphuncle was only slightly subcentral; the center of buoyancy lay adapical to the center of gravity. *b,* juvenile with conch grown beyond a group of closely spaced septa (denoted by spacing of color markings); except for the more subcentral position of the siphuncle, the balance was nearly the same as in the younger animal. *c,* juvenile after truncation of apical section of the cyrtocone; the phragmocone section contained insufficient gas to support the weight of the conch, and the animal was horizontal. *d,* subadult stage before final truncation; gas in the camerae elevated the apical end and weight of the adult ovid part of the conch and the body held down the oral end. *e,* nearly adult stage after secretion of all septa but before final truncation; the siphuncle had already been sealed off at the septum of truncation, the conchiolin behind the septum deteriorated, and openings dissolved into the cyrtocone, letting in water to flood those camerae and weight down that end of the conch; gas filled the camerae in the adult part of the conch. *f,* subadult individual retaining the cyrtocone intact, just after formation of the first ascoceroid septum in the adult ovoid part. *g,* adult after truncation; the cicatrix of attachment appeared as a prominent line; animal shown swimming in normal position. Details of the body are modified after those of *Nautilus.* Tentacles are shown longer than those of *Nautilus* but shorter than those reconstructed for *Orthonybyoceras* by Flower (1955, Fig. 4). It is assumed that this cephalopod propelled itself backward like *Nautilus,* and not forward as suggested for some Paleozoic cephalopods by Schmidt (1930, p. 195) and Flower (1955, pp. 859–60).

bers in certain species was no accidental mutilation, but a habit regularly practised throughout the entire period of growth."

I am convinced that the critical need was to escape the upward pull of gas in the phragmocone and remain nektonic or possibly benthonic. The living *Spirula* floats when at rest, and must swim down into the water (Dunbar, 1924, p. 200); but if the animal could somehow dispose of part of the buoyant gas, it would become a much more efficient swimmer. There is a limit to the positive buoyancy beyond which the cephalopod could not overcome the lifting force, even for brief subsurface excursions. Truncation would solve this problem for the externally shelled animals.

The development of ascoceroid sutures, by which the gas-filled camerae extended over the dorsal side of the conch, was subsequent to truncation. It permitted the animals to attain greater efficiency in swimming. Many authors have pointed out the advantages of the horizontal position of the body in the cephalopod, which travels backward by jet propulsion. Attainment of the horizontal position must invariably be coupled with the maintenance of proper buoyancy; otherwise, it is useless. This was accomplished in cephalopods in diverse ways: (1) by addition of internal deposits near the apical end to counterbalance the weight of the body at the opposite end; (2) by coiling, so that the center of gravity below the center of buoyancy places the body horizontal; and (3) by dorsal migration of the phragmocone. The last seems to be the only way left for a truncated cephalopod. After truncation, the remaining part of the phragmocone is scarcely large enough to have supported the additional weight of adapcal deposits, and coiling to a utilitarian degree is impossible.

Potential buoyancies.—In calculating the buoyancy for various possible forms of *Billingsites noquettensis,* certain assumptions must be made. (1) the specific gravities of shell, body, and sea water were respectively 2.7, 1.08, and 1.03; (2) the complete cyrtocone was 10 cm long; (3) the adapical end of paratype UMMP No. 37813 represents an early septum of truncation; (4) the final septum of truncation was 1 mm thick; and (5) the thickness of the outer wall was proportional to the distance from the apex.

Specimens supply certain measurements of the cyrtocone. As can be seen on steinkerns of adult conchs, the cicatrix, marking the former junction with the cyrtocone, indicates that the adoral end of the conic part was about 2.2 cm wide and 1.4 cm high. A fragment of the outer wall in the only part of the cyrtocone preserved, paratype UMMP No. 37813 (Pl. I, Fig. 9), is about 0.1 cm thick at the adoral end. Although the cyrtocone obviously flared out at its junction with the adult part, it seems reasonable to compare it with an elliptical cone 10 cm long. Of the space within the cone, we may further assume that the living chamber and phragmocone

occupied the same proportions as in the adult part, where they could be approximated with fair accuracy—53 per cent for the living chamber and 47 per cent for the phragmocone. The septa are thin (Pl. II, Fig. 10), and add very little to the total amount of shell material.

With these assumptions we can estimate the buoyancy. The total volume of the conch would be

$$V = \pi RR' \times \text{length}/3 = \pi\ (1.10 \times .70 \times 10/3) = 8.06\ \text{cm}^3$$

and the inside volume, made of the living chamber and phragmocone,

$$L + P = \pi rr' \times \text{length}/3 = \pi\ (1.00 \times .60 \times 10/3) = 6.28\ \text{cm.}^3$$

The shell material would amount to

$$S = 8.06 - 6.28 = 1.78\ \text{cm}^3,$$

the phragmocone

$$P = .47 \times 6.28 = 2.95\ \text{cm}^3,$$

and the living chamber

$$L = .53 \times 6.28 = 3.33\ \text{cm}^3.$$

If the body projected beyond the living chamber by $L/4$ ($= .83\ \text{cm}^3$) then the buoyancy would be

$$B = 1.03\ (V + L/4) - 1.08\ (L + L/4) - 2.7\ S$$
$$= 1.03\ (8.89) - 1.08\ (4.16) - 2.7\ (1.78) = -0.24\text{gm.}$$

This is stage A, for which calculations are entered in Table IV. Thus, if all of the cyrtoconic part were intact, *Billingsites noquettensis* would not float, but could swim with very little effort; it was nearly in equilibrium in the water (see point G in Fig. 5). Thicker shell material in the outer wall, closer spacing of the septa, or decrease in the size of the phragmocone would increase the weight and decrease the buoyancy. It is well to note that the living chamber with 53 per cent of the inside volume would occupy only the adoral 2.23 cm of a conch 10 cm long, and the phragmocone with 47 per cent would occupy the adapical 7.77 cm. The inside radii at the adapical end of the living chamber would be .78 and .47 cm.

If the thickness of shell material remained proportional to the distance from the apex, as assumed, the buoyancy would be also negative for all younger stages of the cyrtocone, and proportional to the cube of the distance from the apex.

It is readily determined that the adapical 7.0 cm of the cyrtocone would have a total volume of 2.77 cm^3, of which 2.16 cm^3 would be phragmocone and .61 cm^3 shell material. From these figures, we can postulate that a cyrtocone 10 cm long upon losing 7 cm by truncation (stage B in Table IV) would become 6.49 times as heavy as the body alone (see point C in Fig. 5).

Before discussing intermediate stages, it is necessary to make the calculations for the adult stage. Upon completion of the cyrtocone, the ceph-

TABLE IV

VOLUMES OF CONCH (V), LIVING CHAMBER (L), PHRAGMOCONE (P), SHELL MATERIAL (S), BODY (L'),* AND TOTAL ANIMAL AND THE RESULTANT BUOYANCY FOR HYPOTHETICAL STAGES OF *Billingsites noquettensis*.

Stage	Complete cyrtocone	Truncated cyrtocone	Incomplete adult conch†	Incomplete adult conch‡	Complete adult conch	Septum of truncation	First ascoceroid septum	All ascoceroid septa	Preseptal gas (1 cm³)§	Measurement							Buoyancy‖	
										Length (cm)	V (cm³)	L (cm³)	P (cm³)	S (cm³)	L' (cm³)	Total (cm³)	B (gm)	B'
A	X	..	..	..	..	..	..	..	..	10.00	8.06	3.33	2.95	1.78	4.16	8.89	−0.14	−0.67
B	..	X	..	..	..	..	..	..	..	3.00	5.29	3.33	0.79	1.17	4.16	6.12	−1.35	−6.49
C	X	..	X	..	..	X	..	..	..	11.75¶	15.60¶	6.61	5.08	3.91	8.26	17.25	−1.71	−4.14
D	..	X	X	..	..	X	..	..	..	4.75¶	12.83¶	6.61	2.92	3.30	8.26	14.48	−2.92	−7.07
E	X	..	..	X	..	X	X	..	..	12.50¶	19.92¶	6.88	8.22	4.82	8.60	21.64	−0.01	−0.02
F	..	X	..	X	..	X	X	..	..	5.50¶	17.15¶	6.88	6.06	4.21	8.60	18.87	−1.22	−2.84
G	..	X	..	X	..	X	X	..	X	5.50¶	17.15¶	5.88	7.06	4.21	8.60	19.87	−0.19	−0.44
H	X	..	..	..	X	X	X	X	..	13.75¶	24.35¶	6.95	11.24	6.16	8.77	26.17	+0.85	+1.94
I	..	X	..	..	X	X	X	X	..	6.75¶	21.58¶	6.95	9.08	5.55	8.77	23.40	−0.36	−0.82
J	..	X	..	..	X	X	X	X	X	6.75¶	21.58¶	5.95	10.08	5.55	8.77	24.40	+0.67	+1.53
K	..	..	..	..	X	X	X	X	..	4.50	17.49	6.95	6.16	4.38	8.77	19.31	−1.41	−3.21
L	..	..	..	..	X	X	X	X	X	4.50	17.49	5.95	7.16	4.38	8.77	20.31	−0.38	−0.87

* Body assumed to have protruded beyond living chamber by one-fifth its volume ($L/4$).
† From Table III: subadult living chamber of 6.61 cm³ would fit into the adapical 2.5 cm of the adult part, enclosed by 2.13 cm³ of shell material, so that the adult part of the conch at stages C and D would have a volume of 8.74 cm³.
‡ From Table III: section of adult part extending 3.25 cm from the apex would have a volume of 13.06 cm³, including 3.04 cm³ of shell material; the first ascoceroid septum would subtend 3.14 cm³ of phragmocone, and the living chamber would occupy the remaining 6.88 cm³.
§ Separation of last ascoceroid septum and posterior ventral aponeurotic band considered evidence of preseptal gas space in adult conch.
‖ Buoyancy expressed as B in grams and as B', the ratio compared with the buoyancy of the body only.
¶ Adult part of conch projects 0.75 cm into the cyrtocone, so that 1.20 cm³ of its volume is enclosed.

alopod begins secretion of the outer wall of the adult; when a band of outer wall sufficient to house the soft parts is finished, the animal draws forward and forms the septum of truncation; thereafter, the adult part is completed by concomitant additions of outer wall and ascoceroid septa. The adult ovoid part of the conch did not accomplish as regular a sequence of growth as did the cyrtocone. Approximations of the volumes of shell, living chamber, and phragmocone must be based on both the dorsoventral and lateral distribution as determined by longitudinal sections and the locations of the sutures on the steinkerns. Of the internal space, about 53 per cent is living chamber and 47 per cent phragmocone.

The adult conch of *Billingsites noquettensis* may be approximated by an elliptical cylinder 5.0 cm long wth radii $R = 1.5$ and $R' = 0.7$ cm. The outer wall and very thin septa would constitute an outer layer averaging .12 cm thick and a basal plate of the same thickness. The inside radii representing the steinkern are $r = 1.38$ and $r' = 0.58$ cm. The total volume of the conch

$$V = 5\ \pi RR' = 16.49\ \text{cm}^3,$$

the shell material amounts to

$$S = 5\ \pi(RR' - rr') + .12\ \pi rr' = 4.22\ \text{cm}^3,$$

and the volume of the living chamber

$$L = .53\ (V - S) = .53\ (12.27) = 6.50\ \text{cm}^3.$$

If one-fifth of the body projected beyond the living chamber, the buoyancy

$$B = 1.03\ (16.49 + 1.63) - 1.08\ (6.50 + 1.63) - 2.7\ (4.22)$$
$$= 18.66 - 8.78 - 11.39 = -1.51\ \text{gm}.$$

A more accurate approach to buoyancy can be made by approximating 0.5 cm segments of the conch and animal by frustra of rectangular pyramids, each frustrum having volume equivalent to the corresponding segment (Table III). My calculations indicate a total volume of the cephalopod $V' = 19.31$ cm^3, shell material $S = 4.38$, phragmocone $P = 6.16$, and body, $L' = 9.11$ cm^3. With these values the buoyancy of the adult (stage K in Table IV) is -1.41 gm or about 3.2 times as heavy as the body alone (point B in Fig. 5). If 1 cm^3 of preseptal gas formed ahead of the last septum (stage K in Table IV) it would support an additional 1.03 gm and thereby raise the buoyancy to -0.38 gm, just slightly lighter than the body itself (point E in Fig. 5).

With the increments of shell, body, and phragmocone computed for each 0.5 cm segment, as listed in Table III, it is possible to compute the amounts of these components at various subadult stages.

If the animal secreted enough of the adult conch to house the living chamber beyond the septum of truncation, while still retaining all of the cyrtocone, it would be in stage C (Table IV). The body may be considered

as somewhat smaller than that of the adult. From Table III it can be determined that a living chamber of 6.61 cm^3 could be housed in the adapical 2.5 cm of the adult part of the conch, and would be enclosed by 2.13 cm^3 of shell material. This does not add quite the total to the volume of the cyrtocone, however, for about 1.20 cm^3 of the adult part projects back into and is enclosed by the cyrtocone. Such a stage would have buoyancy

$$B = 1.03\ (17.25) - 1.08\ (8.26) - 2.7\ (3.91) = -1.71 \text{ gm.}$$

The cephalopod would be a little more than four times as heavy in water as an unshelled form of the same body size.

If the cephalopod at stage C had cast off the adapical 7 cm of the cyrtocone, it would be represented by stage D in Table IV and would have a buoyancy of —2.92 gm (see point D in Fig. 5).

Stage E is a hypothetical form in which the animal has just formed the first ascoceroid septum and retains the entire cyrtocone. From Table III, we can approximate that a living chamber of 6.88 cm^3 would fit ahead of the first ascoceroid septum in an ovoid part 3.25 cm long and having a total volume of 13.06 cm^3. Thus (Table IV) with 4.82 cm^3 of shell, 8.60 of body, and 8.22 of phragmocone, the cephalopod in stage E was nearly in equilibrium.

Stage F is attained by truncation of 7 cm of cyrtocone from stage E. Loss of this part of the phragmocone decreased the buoyancy by 1.21 gm (Table IV).

Stage G is a form in stage F that has added 1 cm^3 of preseptal gas in front of the first ascoceroid septum. This would restore some of the buoyancy, raising it to —0.19 gm.

In stages H–J (Table IV) the specimen has all ascoceroid septa complete; in stage H it retains the complete cyrtocone, in stage I the truncated cyrtocone, and in stage J the truncated cyrtocone and it has added preseptal gas. As shown in Table IV, stages H and J have positive buoyancy—they float. Stage I weighs only about .8 as much as the body alone, and in water has a downward force of .36 gm (point F in Fig. 5).

If our interpretation of UMMP No. 37813 has been correct, it had some preseptal gas and probably was between the hypothetical stages I and J. If it had .35 cm^3 of preseptal gas, it would be in exact equilibrium, according to these computations.

Probable ontogenetic sequence.—Details of the exact progression of stages must remain theoretical, primarily because only one youthful stage is present in the specimens and there is no assurance that it represents a normal individual. If a complete suite of stages could be found, we could proceed with more confidence.

Obviously, however, every *Billingsites noquettensis* had to pass through

the cyrtoconic stage (stage A) in the ontogenetic sequence aimed at the adult ovoid, truncated conch, probably with preseptal gas (stage L). If UMMP No. 37813 is representative, one of the intermediate stages included the complete adult part (with all ascoceroid septa), part of the cyrtocone still attached and some preseptal gas in the back of the living chamber (between stages I and J).

From a cursory inspection of Table IV it is clear that no plausible sequence existed in which the buoyancy remained nearly constant. At one time in its growth, the cephalopod had to secrete the thick septum of truncation as the rear wall of the adult part of the conch, and until the wall was finished it could not have had preseptal gas (stage C or D). If the cyrtocone was truncated, when did such subadult truncation occur? If at the completion of the cyrtocone (stage A to B), B' (the ratio of buoyancy compared to that of the body only) dropped suddenly from -0.67 to -6.49; if after formation of the septum of truncation (stage C to D), B' changed from -4.14 to -7.07; if after formation of the first ascoceroid septum, (stage E to F), from -0.02 to -2.84; and if after completion of the adult part (stages H to I), B' shifted from $+1.94$ to -0.82, and the cephalopod had to spend stage H as a floating animal.

If we postulate that *Billingsites noquettensis* avoided planktonic life throughout its ontogeny, and passed as brief an interval as possible benthonic, then the logical sequence was stage A ($B' = -0.67$), stage C ($B' = -4.14$), stage E ($B' = -0.02$), stage F to G ($B' = -2.84$ to -0.44), stage I to J ($B' = -0.82$ or more), and stage L ($B' = -0.87$). This may be stated as:

(1). From the time it was hatched until the cyrtocone was complete, the individual was lighter in water than a squid of the same size (see Fig. 6*a* and *b*). Potentially, it was an excellent swimmer.

(2). As the animal grew it formed the rear section of the ovoid part of the conch and secreted the thick, heavy septum of truncation. This was probably the only stage in which the cephalopod was bound to the sea floor. The air in the cyrtocone was insufficient to support an appreciable part of the conch and body.

(3). Still retaining the cyrtocone intact, the animal grew forward, at first leaving a preseptal gas space and then secreting the first ascoceroid septum. Then it was nearly in exact equilibrium in the water, so that nearly all of its energy could be utilized for locomotion. The cephalopod was similar to that shown in Fig. 6*f*, but very probably had a shorter cyrtocone.

(4). At this time the cephalopod lost part of the cyrtocone, temporarily increasing its Archimedean weight by loss of that part of the phragmocone.

(5). Very soon, perhaps, the rear wall of the body was drawn adoral, creating a preseptal space that partly compensated for the loss of the apical section of the cyrtocone.

(6). The other two ascoceroid septa were formed, and shortly thereafter the posterior ventral aponeurotic band migrated forward to initiate the adult preseptal gas space. The buoyancy was very close to equilibrium. This is the stage represented by UMMP No. 37813; the cephalopod illustrated in Fig. 6*d* has a longer section of the cyrtocone retained.

(7). As soon as the siphuncle secreted a plug at the septum of truncation, the conchiolin of the shell started deteriorating, aided perhaps by decay of the detached part of the siphon left behind in the cyrtocone. Solution of the aragonite layer then weakened the wall of the cyrtocone further. Possibly, the wall gave way before final truncation and allowed flooding of some of the camerae, as supposed in Fig. 6*e*.

(8). Final truncation produced the adult with an ovoid conch, very light weight in water with about 1 cm^3 of preseptal gas. The cephalopod was nicely streamlined, with the septum of truncation forming the new apex (Fig 6*g*).

The ontogeny outlined here may have been modified by still earlier truncations of segments of the cyrtocone. In general, however, I believe it constitutes a logical interpretation of the life history of *Billingsites noquettensis*.

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Submitted for publication April 18, 1961

PLATES

EXPLANATION OF PLATE I

(All figures natural size)

PAGE

Billingsites noquettensis, sp. nov. 89

FIGS. 1–3. Ventral, dorsal, and right views of steinkern of adult conch. Holotype, UMMP No. 9831.

FIGS. 4–5. Right and ventral views of incomplete steinkern of adult conch. Specimen cut longitudinally to reveal internal structures. Narrow type conch, may be a female. Paratype, UMMP No. 43914.

FIGS. 6–8. Right, ventral, and apical views of incomplete steinkern of adult conch. Ventral view shows a faint crest which may be related to the position of the soft parts at the time of burial. Paratype, UMMP No. 43915.

FIGS. 9–15. Incomplete steinkern of adult part of conch, fragment of outer wall (replaced), and attached steinkern of adoral section of cyrtocone (crushed and distorted). 9–10, ventral and dorsal views of complete specimen. 11–14, apical, right, left, and ventral views of adult part removed from the cyrtocone. 15, ventral view of adult part with probable posterior ventral aponeurotic band (indicated by arrow) and sutures retouched. Paratype, UMMP No. 37813.

PLATE I

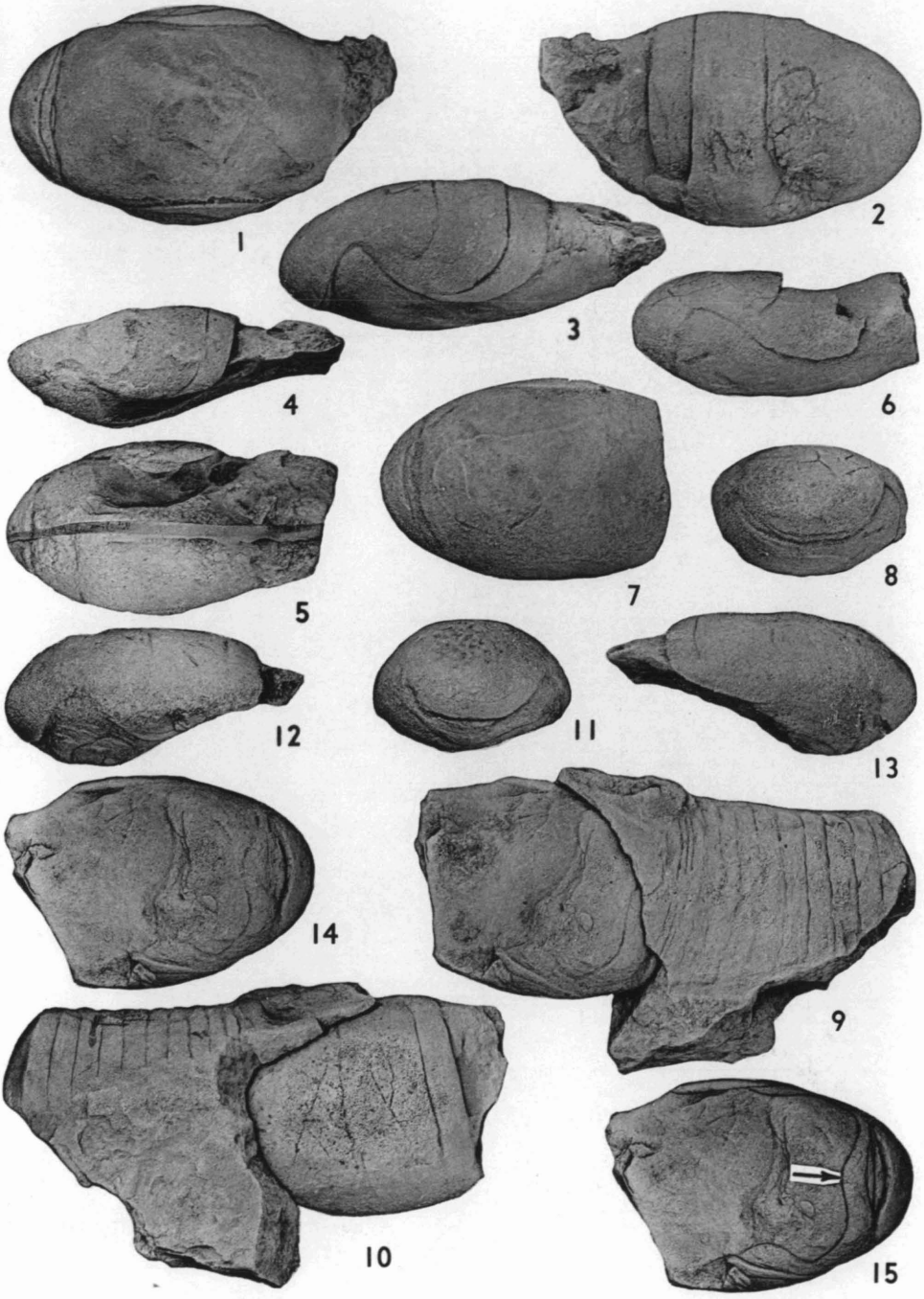
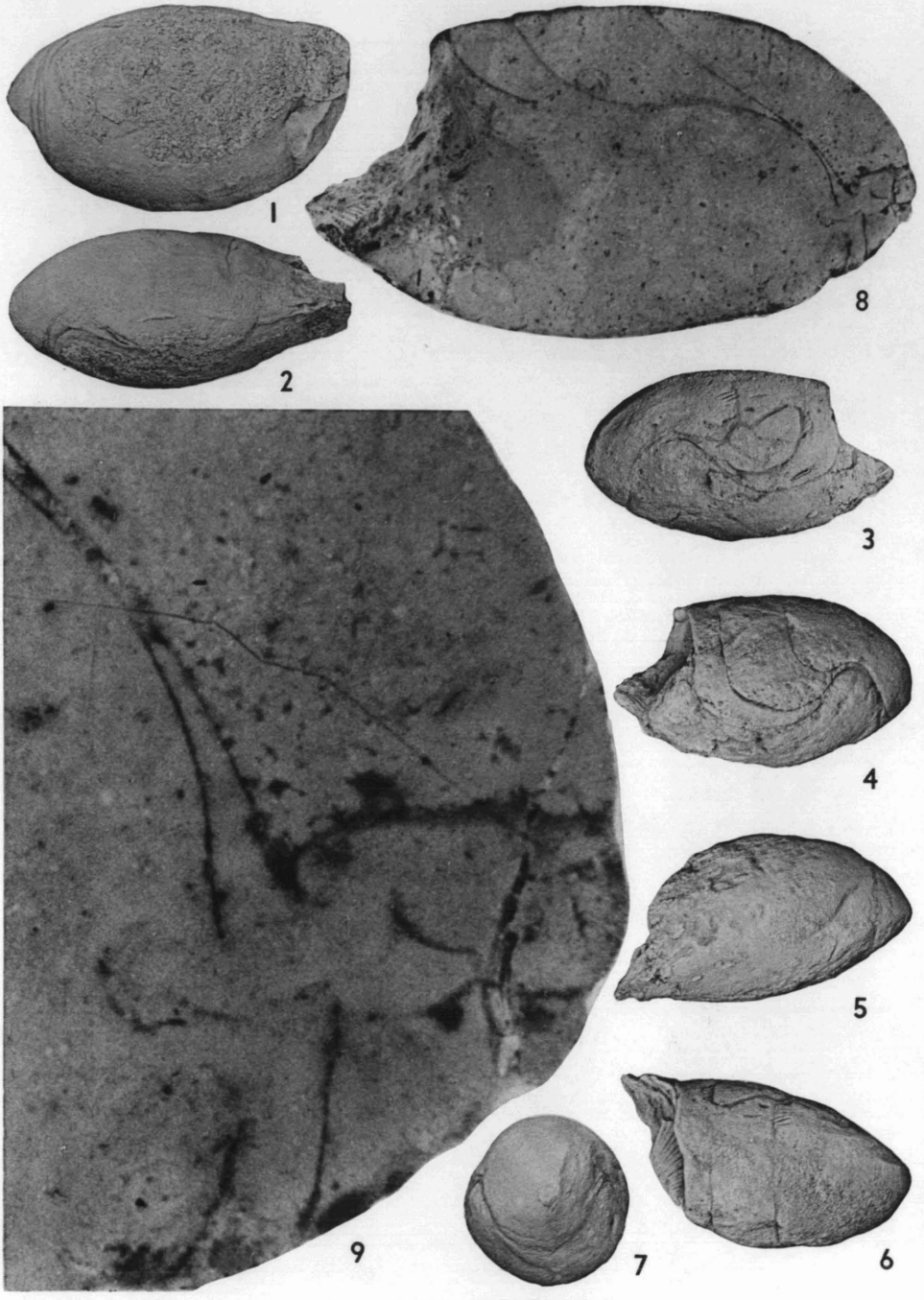


PLATE II



EXPLANATION OF PLATE II

PAGE

Billingsites noquettensis, sp. nov. 89

FIGS. 1–2. Ventral and right views of incomplete steinkern of adult conch. Grooves parallel to ventral and posterior sections of the ascoceroid sutures are probably posterior and anterior ventral aponeurotic bands. Paratype, UMMP No. 43916. x 1.

FIGS. 3–7. Right, left, ventral, dorsal, and apical views of incomplete steinkern of adult conch which was later sectioned (see Figs. 8–9 on this plate). Comparison with living *Nautilus pompilius* indicates that this relatively narrow adult conch may be a female. Paratype, UMMP No. 43917. x 1.

FIGS. 8–9. Polished longitudinal surface, nearly median, UMMP No. 43917 (see Figs. 3–7 above). The siphuncle appears to be constricted between the septum of truncation and the first ascoceroid septum. The third ascoceroid septum does not appear adapically, possibly because the section is not quite median and passes through the lateral position where the third and second ascoceroid septa are fused. Fig. 8, x 2; Fig. 9, x 10.